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MOSQUITO BITING ACTIVITY IN MICHIGAN STATE PARKS AND DEVELOPMENT OF A SYSTEMS SCIENCE MODEL FOR STUDY OF WOODLAND *AEDES*

By

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ABSTRACT

MOSQUITO BITING ACTIVITY IN MICHIGAN STATE PARKS
AND DEVELOPMENT OF A SYSTEMS SCIENCE MODEL
FOR STUDY OF WOODLAND *AEDES*

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Mosquito biting activity was studied in the Michigan park system from 1971 to 1973. Results indicated that woodland *Aedes* mosquitoes were the problem species in the majority of state parks. Adult collections made at North Higgins Lake and Yankee Springs parks in 1972 and 1973 revealed that mosquitoes of the *A. communis-trichurus* and *A. stimulans-fitchii* species complexes, respectively, were the major pests in these two parks. The former complex was a problem at N. Higgins Lake Park with highest biting activity occurring late May and early June. The latter complex was a problem at Yankee Springs Park during most of the summer with biting activity extending until mid-August. Highest activity for the two-year study occurred during June and July. The sampling trials at each park were conducted at three areas designated for public use and at peak biting levels recreational activities were cancelled by park personnel. Field investigations into specific areas of *A. stimulans-fitchii* population dynamics was also conducted. A representative breeding site was surveyed during 1972 and 1973 and data on instar

composition and developmental rates were collected. Information on adult female longevity was also obtained. Immature and adult mortality rates were estimated for a population cohort, larval densities were calculated, and female egg input response was redefined.

Research dealt, in part, with the construction of a system model which gave a description of the dynamic behavior of this insect group. This approach was essentially a sequential structuring process involving the following: a definition of the system and its components; determination of the behavioral features and their causal orientations for each component of the system; the constraints by which the components are governed; and free body modeling of each component. Since the model will be used as an aid in developing larval control strategies, emphasis was placed on the interaction between the aquatic environment and the immature life stages. As a result behavioral features involving these interactions were chosen for inclusion in the model. Features of the aquatic environment were viewed as stimuli to the biological components of interest while the response variables were aspects of the Aedes life cycle which would reflect the effects of control measures.

A computer simulation implementing this model was constructed and refined utilizing results from population studies of A. stimulans-fitchii mosquitoes. Information and data utilized in the model construction were obtained from surveys conducted in Michigan state parks and an extensive literature review. Dynamics of the mosquito's life cycle and of the woodland pool ecosystem were modeled and the resultant equations are described. Assumptions used in the modeling process are briefly discussed in order to show the reasoning process underlying the use of these equations in the simulation. A description of computer program structure and data files utilized by the program is given. Research on and refinement of the physical components consisted of measurements during 1973 on aquatic parameters chosen as key factors in immature mosquito dynamics and meteorological features oriented as stimuli to these parameters. The resultant data were statistically analyzed to obtain the best available model for maximum water temperature, dissolved oxygen concentration, and water depth.

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GENERAL INTRODUCTION

A research program was proposed by representatives of the Michigan Department of Natural Resources to study mosquito and other biting insect problems of state parks and recreational areas. The proposal of this study was due to concern that existing mosquito control efforts in park areas merited a complete reevaluation. Unsuccessful attempts in the past to regulate these biting insects made it imperative that studies on species composition, relative abundance, and seasonal distribution be undertaken. As temporary woodland pools in the park areas are utilized as breeding sites by certain species of Aedes mosquitoes, a research project concerning interaction of the immature life stages with these aquatic ecosystems was also proposed.

Previous research (Horsfall et al., 1958; Horsfall, 1963; Horsfall and Trpis, 1967) has shown that inundation of the breeding sites, a threshold water temperature, and reduced oxygen tension are necessary stimuli for final egg hatch. Hatching in the field occurred when the water temperature rose above 5° C. The dynamics of decreasing oxygen content in a temporary woodland pool is not well understood (Ruttner, 1963). In the larval stage the influence of water temperature on the rate of development has been researched by Anderson and Horsfall (1969) and Trpis and Horsfall (1969). Results indicated that the range of temperature that promotes normal growth for two species of woodland Aedes mosquitoes was 5° to 21° C. Length of larval development as well as instar duration depended on water temperature. Any temperature in excess of 21° C had an adverse effect on the maturing mosquito either in increased mortality or eventual supression of male characteristics. McDaniel (1958) observed that development from hatching to emergence of A. stimulans required 13 to 60 days, depending on temperature. Biological control of A. stimulans in woodland pools was researched by James (1961) who observed that adult dytiscids and immature Limnephilis sp. were predators of early instar larvae. Mermithid nematode parasitism of the same mosquito species complex was studied by Hagan (1966) and Dayton (1971).

Adults of woodland Aedes mosquitoes are found in highest density adjacent to pool areas and will disperse 200 to 300 yards (McDaniel, 1958). Defoliart et al. (1967) has reported that biting activity for the A. stimulans complex in Wisconsin began in mid-May, peaked during June, and existed through July and August. Hagan (1966) reported similar biting activity for this species complex in Michigan. Woodland Aedes females initiate biting activity 10 to 15 days after emergence with successive portions of the population laying eggs throughout the season until August (Detinova, 1968). Eggs are deposited on moist layers of plant detritus along the flood line of woodland pool micro-basins (Horsfall, 1963). The woodland Aedes group as represented by the A. stimulans and A. communis species complexes are univoltine with egg diapause shown to be obligatory (Horsfall and Fowler, 1961). Adult distribution for the *Aedes* woodland group is throughout Michigan (Pedersen, 1947) with the *A. stimulans* complex most abundant in the southern lower peninsula and *A. communis* complex more prevalent in northern Michigan (Irwin, 1942). A recent study by Gorton (1973) showed that woodland *Aedes* mosquitoes were collected in substantial numbers at a southern Michigan subdivision.

Due to the sheer complexity of the relationship between the aquatic environment and immature life stages of woodland *Aedes* mosquitoes, a systems science approach was undertaken. Systems ecology has shown that ecosystems can be modeled usefully and the value of the modeling process justifies the effort. The result has been a coordinating effect on organizing research projects as well as clarifying components of an ecosystem, identifying data requirements and determining research priorities. Given a model developed according to this approach and utilizing requirements of these mosquitoes, a computer simulation was one of the methods available for examining behavior and effects of external stimuli. The weakness of many computer simulation studies is that they provide little more than a tabulation of particular or overall behavior of the system. The use of systems science in imparting an internal structure to the simulation model can result in the elimination of such defects. As a result, a framework could be provided upon which to base decisions concerning steps to be taken in altering the system to obtain adequate pest management of this mosquito. The accuracy of these predictions would depend on how well the simulated model represented biological reality. Continual comparison with the natural ecosystem would be required to adequately validate the simulation model.

In view of these considerations, a research project was conducted in the Michigan park system during 1971-1973 with the following objectives: (1) conduct mosquito surveys in the Michigan state park system; (2) study the relationship between the aquatic environment and immature life stages of woodland *Aedes* mosquitoes; (3) construct a simulation model of the woodland *Aedes* ecosystem utilizing a systems science approach.

PART I

SURVEY OF MOSQUITO BITING ACTIVITY IN MICHIGAN STATE PARKS AND A STUDY OF *AEDES STIMULANS-FITCHII* POPULATION DYNAMICS[1]

INTRODUCTION

Adult mosquito surveys were conducted in selected Michigan state parks during 1971-1973. The primary objectives were to determine the human-biting species present at public use areas and to study the duration and intensity of mosquito biting activity. The need for studies on species composition, relative abundance, and seasonal distribution was emphasized due to increased awareness of potential arthropod disease activity as well as widespread disruption of human recreational activities.

Studies were also conducted during 1972 and 1973 on populations of the *Aedes stimulans-fitchii* species complex. An important consideration in understanding population dynamics of this mosquito was comprehension of immature stage--aquatic breeding site interactions. If these interactions were better understood, then insights into the regulation of population densities could be elucidated. Accordingly, biological analysis would provide a framework upon which to base decisions concerning strategies to be taken in altering the *Aedes* ecosystem to obtain adequate management of this pest.

SURVEY METHODS

Adult Mosquito Studies

In 1971 eleven park areas (Fig. 1) in Michigan were chosen for mosquito surveys that included adult landing and biting collections. Park naturalists conducted the surveys in public use areas within each park. The collections were sent to the medical entomology laboratory at Michigan State University for identification. Based upon this survey North Higgins Lake and Yankee Springs, recreation areas located in north central and southern Michigan, respectively, were selected for further studies. Biting collections were continued at these two parks in 1972 and 1973. North Higgins Lake Park is located on the northern end of Higgins Lake in a hardwood and pine forested area and is 428.94 acres in size. The Yankee Springs recreational area is located on Gun Lake and comprises 4,971.57 acres in a maple and oak hardwood forest region. The biting count collections were standardized as follows:

1. Collections were started with the emergence of the *Aedes* snowpool group and conducted every seventh day until the mean biting count was <10 per 10 minute sampling period for two consecutive sampling trials.
2. Collections were made at three public use areas: nature trail, campground, and outdoor education center.

3. Collections were made during the morning hours between 8:00-10:00 a.m.
4. Mosquitoes collected were either probing or actually feeding on the collector.

Immature Mosquito Studies

Field research was also conducted during 1972 and 1973 on immature mosquito populations at Yankee Springs recreational area in southwestern Michigan. Investigations into specific areas of population dynamics was indicated by a lack of data and/or information concerning this species complex's ecosystem. As a preliminary survey of four woodland pools in the park indicated uniform larval densities among pools, a representative breeding site was chosen for in-depth surveys (Wagner).[2] It consisted of an oval microbasin area subject to seasonal, temporary flooding with maximum flood occurring in early spring. This flooding produced an estimated surface area of 2,364 sq. ft. and provided suitable habitat for the hatch and development of the immature stages. Larvae and pupae were collected during and after periods of maximum flood along four transect lines at right angles to the long axis of the pool. During 1972, samples were taken at 7 day intervals beginning April 14 and ending May 10. A total of 24 water samples representing 2.73 sq. ft. of surface area was taken at each trial. In 1973 the procedure was repeated except that 60 samples were taken at each trial (representing 8.18 sq. ft. of surface area) and the sampling period extended from March 27 to April 24 due to earlier egg hatch.

RESULTS

Adult Mosquito Collections

A total of 848 adult mosquitoes submitted from the 10 state parks were identified (no adult specimens were submitted from North Higgins Lake) in 1971 to determine the species composition and frequency of occurrence throughout the park system. Table 1 lists the species of mosquitoes identified from landing and biting collections made in the 10 parks during 1971. The *Aedes* snowpool group was the most abundant species group collected in seven parks (range 40.0% in park 8 to 90.2% in park 2) while *Coquillettidia perturbans* constituted 76.5 and 92.3 percent in parks 9 and 11 and *Anopheles quadrimaculatus* comprised 46.4 percent of the sample from park 5. *Aedes vexans*, *Aedes triseriatus* and *Culex pipiens* made up the remaining portion of the sample population. Frequency of occurrence and the percentage of the total number of collections in which a certain species or species group occurs is also shown in Table 1. The *Aedes* snowpool group and *C. perturbans* had the highest frequency of occurrence, being present in 90 percent of the park samples. During the same collection periods *A. vexans* was present in 50 percent of the samples while *A. quadrimaculatus* and *A. triseriatus* showed a frequency of occurrence of 40 percent *C. pipiens* had the lowest frequency of occurrence of 30 percent in the park collections.

The Aedes snowpool group was further analyzed to species and species complex for each park collection. The results are shown in Fig. 2. The A. stimulans complex was most abundant in seven parks, comprising 100 percent of the snowpool group in four park areas. The A. communis complex was present in samples submitted from three northern parks, being the most abundant in park 2 (73.15%). A. canadensis was the most abundant in park 3 where it comprised 68.2 percent of the sampled Aedes snowpool group. The least abundant of this group was A. cinereus in parks 2, 3, and 10 (12.1, 13.6, and 10.4%) and A. trivittatus in park 1 (2.9%).

Adult biting collections during 1972 and 1973 showed that individuals of the Aedes communis-trichurus complex were the problem mosquitoes at North Higgins Lake Park while an identical sampling program conducted at Yankee Springs recreational area indicated that mosquitoes of the A. stimulans-fitchii complex were responsible for biting problems there. Identification of these collections was aided by keys contained in Barr (1958) and Carpenter and LaCasse (1955). Tables 2 and 3 show the results of the two-year study on biting activity at the two parks. The highest activity for A. communis-trichurus occurred in late May and early June with a mean count per site $\geq$ 20 mosquitoes per 10 minutes. Biting activity was reduced approximately 50 percent by the fourth sampling both years. A mean count of $<$ 10 mosquitoes was recorded during the July 6 sampling in 1972 while a similar level in 1973 occurred three weeks earlier, on June 14. The biting activity for this species complex for both years was essentially non-existent after the third week in July. Other species identified from the biting collections from North Higgins Lake were A. canadensis, A. triseriatus, A. stimulans complex, A. vexans and C. perturbans. Of these only A. canadensis was consistently present in the collections beginning the first week in June and lasting through the July collections. The mean biting count for this species in 1972 ranged from 4.67 in the July 6 collections to 2.00 during the July 20 collecting period while in 1973 the mean count ranged from 5.67 on July 5 to < 1.00 on August 2. C. perturbans was collected in substantial numbers from only one site during 1972 and 1973. Individuals of this species appeared in the collections during the first week of July both years with the highest count of 14 for a 10 minute sampling trial recorded July 13, 1972 at the outdoor educational site. However, the species was never detected on a regular basis at any of the other sites. The other previously mentioned species were present so infrequently and in such small numbers that their contribution to the biting problem was considered minimal.

Table 3 shows the results of the two-year sampling study at Yankee Springs recreational area for the A. stimulans-fitchii complex. The adult population had completely emerged by the end of May 1972 and the mean biting activity per site for seven weekly sampling trials ranged from 66.33 mosquitoes on July 4 to 51.00 mosquitoes on July 18. During the last week in July and first week in August the mean biting activity per site dropped to 35.67 and 31.67, respectively. During and after the second week in August the mean biting activity per site was < 10 mosquitoes. The biting activity of the A. stimulans-fitchii complex during 1973 was similar. The average level of biting activity during the same time period ranged from (samples taken a day later from the 1972 trials) 20.67 to 70.33. The mean biting activity from July 19 to August 2 was above 20.00. During the sampling trials on August 9 and 16 the mean count dropped to below 10 per site. Other species identified from the biting collections were A. canadensis, A. vexans, A. cinereus, A. communis complex, C. perturbans and Anopheles walkeri. Of these, A. canadensis and A. vexans were consistently collected in large numbers from the three public use sites during 1972 and 1973. Although A. canadensis was collected in sampling trials 1 through 78 both years the mean biting count for the three sites never exceeded 10 mosquitoes with the average biting activity for 1972 and 1973 being 3.67 and 6.52, respectively. A. vexans was present from the second week in June until the end of July both years with a high count of 8.33 recorded on June 28, 1973.

Comparison of Biting Activity and Effect on Recreation

The level and duration of biting activity of the two species complexes were quite different. Figs. 3 and 4 show the biting activity for 1972 and 1973 at North Higgins Lake and Yankee Springs park areas, respectively. The ordinate scale measuring biting activity is of the same magnitude in both graphs and represents an average total of mosquitoes collected for each sampling trial during the two year study.

The average total of mosquitoes collected at North Higgins Lake during the first three trials was 74.50, 75.70 and 61.50, respectively. During the next three sampling trials mosquitoes collected averaged 26.50, 30.50, and 30.00 with the remaining samples in July averaging < 20 mosquitoes. At Yankee Springs during peak biting activity for A. stimulans-fitchii complex, the average number collected ranged from 154.00 to 200.00 over a seven week sampling period (sampling trials 1-43). This was more than twice the average number collected at peak biting levels and more than a twofold increase in the duration of biting activity as compared with the A. communis-trichurus complex at North Higgins Lake. While the mosquitoes collected at Yankee Springs averaged 89.00 by the last week in July, this level was still comparable to peak biting activity at North Higgins Lake during late May and early June. Finally the average number of mosquitoes collected during the last two sampling trials (71 and 78) at Yankee Springs was 27.00 and 18.50, respectively. Comparable values for the A. communis-trichurus complex at North Higgins Lake occurred approximately a month earlier.

Preliminary observations on the effect of biting activity on human recreation were also carried out. Fig. 3 shows that peak park attendance at North Higgins Lake occurred during late June, July and August when the mean biting count was < 10 mosquitoes per site. When the mean biting collections during late May were ≥ 20, park visitors avoided recreational sites located in forested regions (i.e., nature trails) and stayed in those localities that possessed good prevailing winds (lake fronts) and lacked a forest canopy (beach areas). When the mean biting counts were ≤ 10 during June the recreational sites in these forested areas were utilized by park visitors.

Recreational activities at nature trail and outdoor educational areas in Yankee Springs were adversely affected by the biting activity of *A. stimulans-fitchii* mosquitoes until the first week in August when mean counts dropped to ≤ 20.00 mosquitoes. The biting annoyance at the nature trail became so intense during late June and July 1973 that the park naturalist cancelled planned recreational activity for this area, mainly group tours for the purpose of nature studies. Biting collections made during this time showed a mean count of approximately 70 mosquitoes per site. A high of 84 mosquitoes was collected in a 10 minute period at the nature trail on June 28, 1973. Fig. 4 shows that park attendance and mosquito biting activity peak essentially at the same time and at levels much higher than at North Higgins Lake.

Dynamics of a Woodland Aedes Species Complex

Table 4 shows the composition of the immature stages of *A. stimulans-fitchii* at Yankee Springs in 1972. All collected on April 12 were either first or second instars with the latter representing 57.4 percent of the total. In the second collection 12 or 21.4 percent had matured to the third instar while 30 were in the first instar. All stages (I-IV) were present in the April 26 sample with fourth instars comprising 7.3 percent of the total and present for the first time. Immature development was rapid from April 26 to May 10. Of the

27 collected on May 3 all larvae were either third or fourth instars with the former comprising 62.9 percent of the total. The last collection made on May 10 contained only fourth instars and pupal stages, each representing approximately 50 percent of the total. No first or second instars were present in the last two trials and adult emergence was first observed May 11 and continued for seven days.

Egg hatch occurred earlier in 1973 than in 1972 (Table 5). The first collection made on March 31 contained primarily first and second instars although approximately 2 percent had progressed to the third instar. The number of first instar present in the April 3 sampling trial increased substantially (335 as compared with 94 the previous week) with 76.5 percent of the total being at this stage of development. In the third trial all larval stages were present with 69.8 percent in the second, 22.9 percent in the third and approximately 2 percent in the fourth stage of development. The fourth collection on April 17 contained instars two through four with the majority (71.7%) still in the second stage. Fourth instars had increased to 5 percent. The last samples contained 76.3 percent fourth instar larvae and 8.5 percent in the pupal stage. Adult emergence was first observed a week later on May 1 and continued for approximately 9 days. In addition, estimates were made on immature population densities in the aquatic microbasin area. The method used utilized the numbers collected and the size of the habitat area. Larvae and pupae counts were multiplied by a factor obtained from the following proportion to estimate the absolute density: total surface area/total surface area sampled. The resultant values are shown in parentheses below the actual sample values in Tables 4 and 5.

Immature and Adult Mortality

Mortality rates for immature stages were obtained from life tables (Table 6) utilizing data contained in Tables 4 and 5. During 1972 mortality was estimated as increasing from 0.082 during the first age interval to 0.445 for the last. Mortality for the 28 day period was 0.754. Overall mortality in 1973 was estimated as 0.731 with no mortality estimated within the first age interval. Rates of 0.283, 0.179 and 0.543 were calculated for the remaining intervals. The substantial late instar mortality observed during 1972 and 1973 was due largely to inadequate nutritional resources in the woodland pool breeding sites (Cummins).[3] These depositional aquatic systems contained a variety of fine particle detritus utilized as food by mosquito larvae. As nutritional requirements increase significantly for successive developmental stages, the amount of available detritus was seen as a limiting factor. Although a chaoborid, *Mochlonyx sp.*, a predator of mosquito larvae, was consistently sampled throughout the two-year study, developmental rates of both insects were in phase and no significant mortality was observed. This suggested that the *A. stimulans-fitchii* ecosystem was essentially predator free during 1972 and 1973.

Values for adult mortality were obtained from life tables (Table 7) utilizing data from biting insect studies in 1972 and 1973 at Yankee Springs recreational area. As the surveys were conducted beneath a dense forest canopy, adverse weather conditions had minimal effect on biting activity. Similar biting counts for A. stimulans-fitchii at different collection sites indicated the mosquitoes were regularly distributed throughout the park. Research (Detinova, 1968) has also shown that univoltine, early season Aedes mosquitoes surviving to August completed 6 gonotrophic cycles indicating a requirement for successive blood meals during the summer months. For these reasons, substantial departures from peak biting levels were considered a result of mortality factors affecting the mosquito population. Conversely, mortality was considered minimal at peak biting levels (age intervals 0-36). Life tables for adult A. stimulans-fitchii show that a population cohort is long lived with 0.12 surviving to age interval 78-85 in 1972. During the same time period in 1973, 0.059 were estimated as surviving. In terms of actual time of year, this age interval represents the second week in August. Since this species complex is univoltine and adult emergence was complete by May 31, females surviving to the last age interval were approximately three months old. Zero mortality was assumed for one month after emergence. Empirical observations indicated that adult males were present for approximately two weeks after initial female emergence.

Footnotes

[1]Journal article no. 6906, Michigan Agricultural Experiment Station. This research was supported by a fellowship grant from the Michigan State Department of Natural Resources.

[2]V. Wagner. Data from a completely randomized transect sampling procedure was analyzed by a nested analysis of variance. The variance component due to pools was not significant at the .05 or .01 levels (unpublished data).

[3]K. Cummins. Personal communication, September 1973.

Table 1. Percent composition of the major mosquito species in landing/biting collections made in ten state parks, 1971

Park	Total No.	*Aedes* snow-pool group	*Coquillettidia perturbans*	*Aedes vexans*	*Anopheles quadrimaculatus*	*Aedes triseriatus*	*Culex pipiens*
1	70	50.0	32.9	1.4	--	7.1	7.1
2	367	90.2	1.1	7.4	--	1.3	--
3	28	88.0	12.0	--	--	--	--
4[a]	--	--	--	--	--	--	--
5	112	30.4	< 1.0	10.7	46.4	--	--
6	81	58.0	2.5	6.2	28.4	4.9	--
7	21	80.9	19.1	--	--	--	--
8	30	40.0	--	--	30.0	--	23.3
9	53	--	92.3	--	7.7	--	--
10	69	42.0	20.3	23.2	--	10.1	4.4
11	17	23.5	76.5	--	--	--	--

[a]No adult samples submitted from North Higgins Lake.

Table 2. Biting activity of *Aedes communis-trichurus* complex at North Higgins Lake state park, 1972-1973

Month/Day[a]		Sampling Trial	Sample Total		$\bar{x}$ Biting Count/10 Min		$S_{\bar{x}}$	
1972	1973	1 Week Interval	1972	1973	1972	1973	1972	1973
May 25	24	1	81	68	27.00	22.67	2.646	2.186
31	31	8	86	65	28.67	21.67	2.404	1.732
June 8	7	15	64	59	21.33	19.67	1.764	2.028
15	14	22	29	24	9.67	8.00	1.453	1.000
22	21	29	35	26	11.67	8.67	1.856	1.453
29	28	36	31	29	10.33	9.67	0.882	1.856
July 6	5	43	19	16	6.33	5.33	0.333	0.333
13	12	50	28	10	9.33	3.33	0.882	0.882
20	19	57	5	--	1.67	--	0.667	--

[a]Collections made at weekly intervals from time of adult emergence until mean biting count per site was <10/10 min. period for two successive weeks.

Table 3. Biting activity of <u>Aedes</u> <u>stimulans-fitchii</u> complex at Yankee Springs recreational area, 1972-1973

Month/Day[a]			Sampling Trial	Sample Total		$\bar{x}$ Biting Count/10 Min		$S_{\bar{x}}$	
1972		1973	1 Week Interval	1972	1973	1972	1973	1972	1973
May	31	31	1	168	141	56.00	47.00	4.163	10.017
June	6	7	8	181	175	60.33	58.33	4.631	8.212
	13	14	15	190	199	63.33	68.67	3.283	7.311
	20	21	22	189	195	63.00	65.00	3.055	7.056
	27	28	29	185	211	61.67	70.33	3.844	8.413
July	4	5	36	199	201	66.33	67.00	4.177	7.371
	11	12	43	176	157	58.67	52.33	8.110	10.493
	18	19	50	153	62	51.00	20.67	6.028	2.603
	25	26	57	107	71	35.67	23.67	8.090	2.667
Aug.	1	2	64	95	63	31.67	21.00	7.688	5.132
	8	9	71	29	25	9.67	8.33	0.667	2.028
	15	16	78	25	12	8.33	4.00	0.882	1.000

[a]Collections made at weekly intervals from time of adult emergence until mean biting per site was < 10/10 min. period for two successive weeks.

Table 4. Immature *Aedes stimulans-fitchii* in a woodland pool at Yankee Springs recreational area, 1972

Date	Sampling Trial	No. of Larval Instars (I-IV) & Pupae (P)					Total
		I	II	III	IV	P	
4/12	1	26 (22,515)[a]	35 (30,308)				61 (52,823)
4/19	2	30 (25,979)	14 (12,123)	12 (10,391)			56 (48,493)
4/26	3	14 (12,123)	12 (10,391)	12 (10,391)	3 (2,598)		41 (35,503)
5/3	4			17 (14,721)	10 (8,660)		27 (23,381)
5/10	5				8 (6,928)	7[b] (6,062)	15 (12,990)

[a]Estimated total number of larvae in woodland pool in parenthesis.

[b]Adult emergence first observed on 5/11/72 and completed 5/17/72.

Table 5. Immature *Aedes stimulans-fitchii* in a woodland pool at Yankee Springs recreational area, 1973

Date	Sampling Trial	No. of Larval Instars (I-IV) & Pupae (P)					Total
		I	II	III	IV	P	
3/27	1	94 (27,166)[a]	41 (11,849)	2 (578)			137 (39,593)
4/3	2	335 (96,815)	94 (27,166)	9 (2,601)			438 (126,582)
4/10	3	17 (4,913)	219 (63,291)	72 (20,808)	6 (1,734)		314 (90,746)
4/17	4	185	60 (53,465)	13 (17,340)	(3,757)		258 (74,562)
4/24	5			18 (5,202)	90 (26,010)	10[b] (2,890)	118 (34,102)

[a]Estimated total number of immature stages in woodland pool.

[b]Adult emergence first observed on 5/1/73 and completed by 5/10/73.

Table 6. Life tables for immature *Aedes stimulans*-*fitchii* in a woodland pool ecosystem at Yankee Springs recreational area, 1972-1973[a]

Age Interval (Days) x	No. Surviving at Start of x l_x		No. Dying Within Interval x to x + 1 d_x		Mortality Rate q_x[b]		Survival Rate p_x[c]	
0	1,000	1,000	82	0	0.082	0.000	0.918	1.000
7	918	1,000	246	283	0.268	0.283	0.732	0.717
14	672	717	229	128	0.341	0.179	0.659	0.821
21	443	589	197	320	0.445	0.543	0.555	0.457
28	246	269	--	--	--	--	--	--

[a]The two columns under each heading are for the years 1972 and 1973, respectively.

[b]Overall mortality rates for 1972 and 1973 are 0.754 and 0.731, respectively

[c]Overall survival rates for 1972 and 1973 are 0.246 and 0.269, respectively.

Table 7. Life tables for adult *Aedes stimulans-fitchii* at Yankee Springs recreational area, 1972-1973[a]

Age Interval (Days) x	No. Surviving at Start of x l_x		No. Dying Within Interval x to x + 1 d_x		Mortality Rate q_x		Survival Rate p_x	
0-36	1,000	1,000	0	0	0.000	0.000	1.000	1.000
36	1,000	1,000	156	219	0.156	0.219	0.884	0.781
43	844	781	110	473	0.131	0.606	0.869	0.394
50	734	308	221	0	0.301	0.000	0.699	1.000
57	513	308	58	0	0.112	0.000	0.888	1.000
64	455	308	316	186	0.695	0.603	0.305	0.397
71	139	122	19	63	0.138	0.520	0.862	0.480
78	120	59	120	59	1.000	1.000	0.000	0.000
85	0	0	--	--	--	--	--	--

[a]The two columns contained under each heading are for the years 1972 and 1973, respectively.

Fig. 1. Park and recreational areas in Michigan where mosquito surveys were conducted during 1971. Size in acres of each park is as follows: 1--58,327.2; 2--19,244.5; 3--9,138.0; 4--428.0; 5--196.3; 6--963.0; 7--981.0; 8--9,612.6; 9--17,053.2; 10--4,971.6; 11--4,156.6.

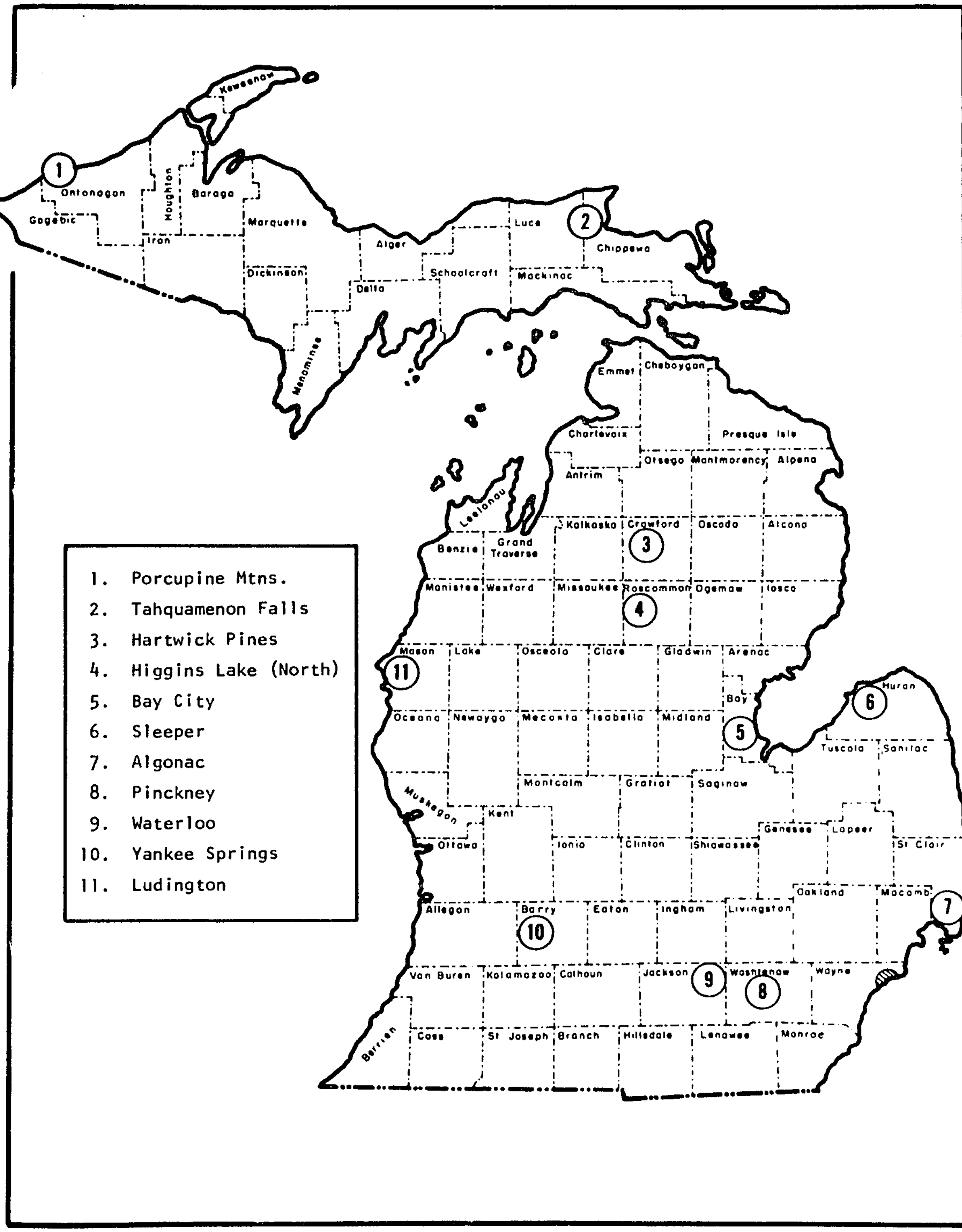
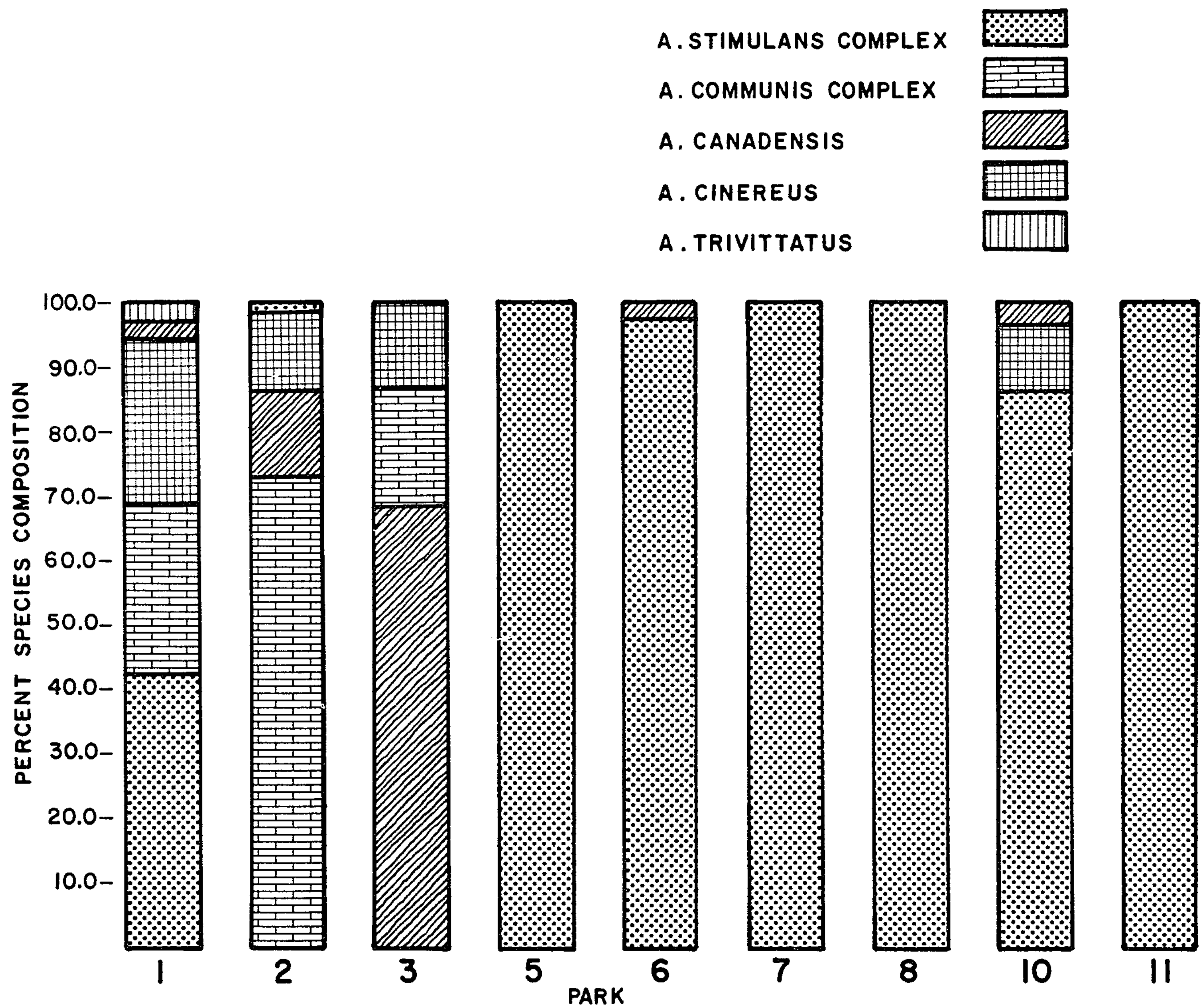

1. Porcupine Mtns.
2. Tahquamenon Falls
3. Hartwick Pines
4. Higgins Lake (North)
5. Bay City
6. Sleeper
7. Algonac
8. Pinckney
9. Waterloo
10. Yankee Springs
11. Ludington
Keweenaw
Ontonagon
Gogebic
Houghton
Baraga
Iron
Marquette
Dickinson
Menominee
Delta
Alger
Schoolcraft
Luce
Mackinac
Chippewa
Emmet
Cheboygan
Charlevoix
Presque Isle
Antrim
Otsego
Montmorency
Alpena
Leelanau
Benzie
Grand Traverse
Kalkaska
Crawford
Oscoda
Alcona
Manistee
Wexford
Missaukee
Roscommon
Ogemaw
Iosco
Mason
Lake
Osceola
Clare
Gladwin
Arenac
Huron
Bay
Oceana
Newaygo
Mecosta
Isabella
Midland
Tuscola
Sanilac
Montcalm
Gratiot
Saginaw
Muskegon
Kent
Genesee
Lapeer
Ottawa
Ionia
Clinton
Shiawassee
St Clair
Oakland
Macomb
Allegan
Barry
Eaton
Ingham
Livingston
Van Buren
Kalamazoo
Calhoun
Jackson
Washtenaw
Wayne
Berrien
Cass
St Joseph
Branch
Hillsdale
Lenawee
Monroe

Figure 1

Fig. 2. Percent species composition of the *Aedes* snowpool mosquitoes identified from collections made in nine Michigan state park and recreational areas, 1971.



A. STIMULANS COMPLEX
A. COMMUNIS COMPLEX
A. CANADENSIS
A. CINEREUS
A. TRIVITTATUS
PERCENT SPECIES COMPOSITION
100.0
90.0
80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
1
2
3
5
6
7
8
10
11
PARK

Figure 2

Fig. 3. Average mosquito biting activity and park attendance for 1972 and 1973 at North Higgins Lake state park.

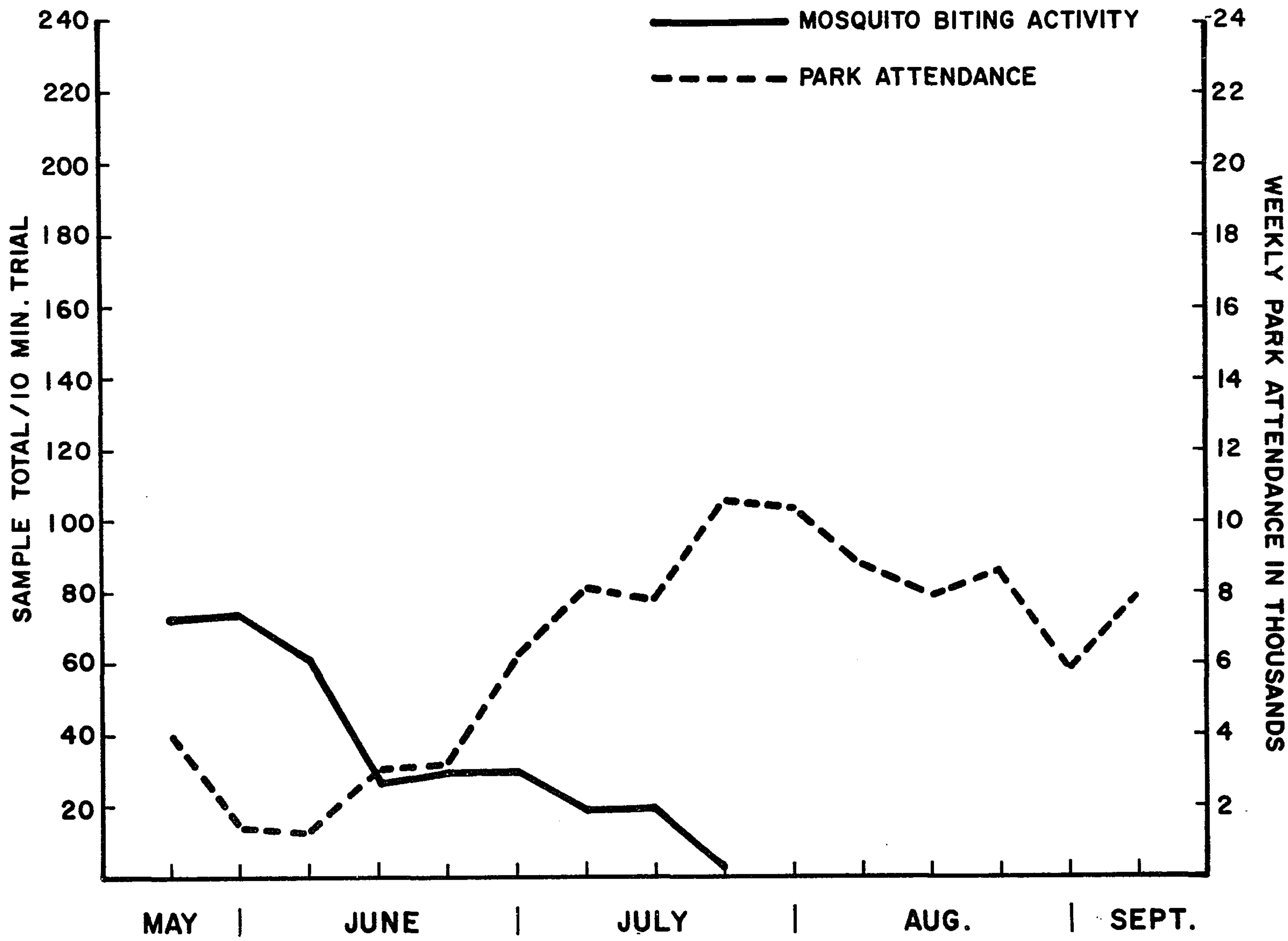

MOSQUITO BITING ACTIVITY
PARK ATTENDANCE
SAMPLE TOTAL/10 MIN. TRIAL
240
220
200
180
160
140
120
100
80
60
40
20
WEEKLY PARK ATTENDANCE IN THOUSANDS
24
22
20
18
16
14
12
10
8
6
4
2
MAY
JUNE
JULY
AUG.
SEPT.

Figure 3

Fig. 4. Average mosquito biting activity and park attendance for 1972 and 1973 at Yankee Springs recreational area.

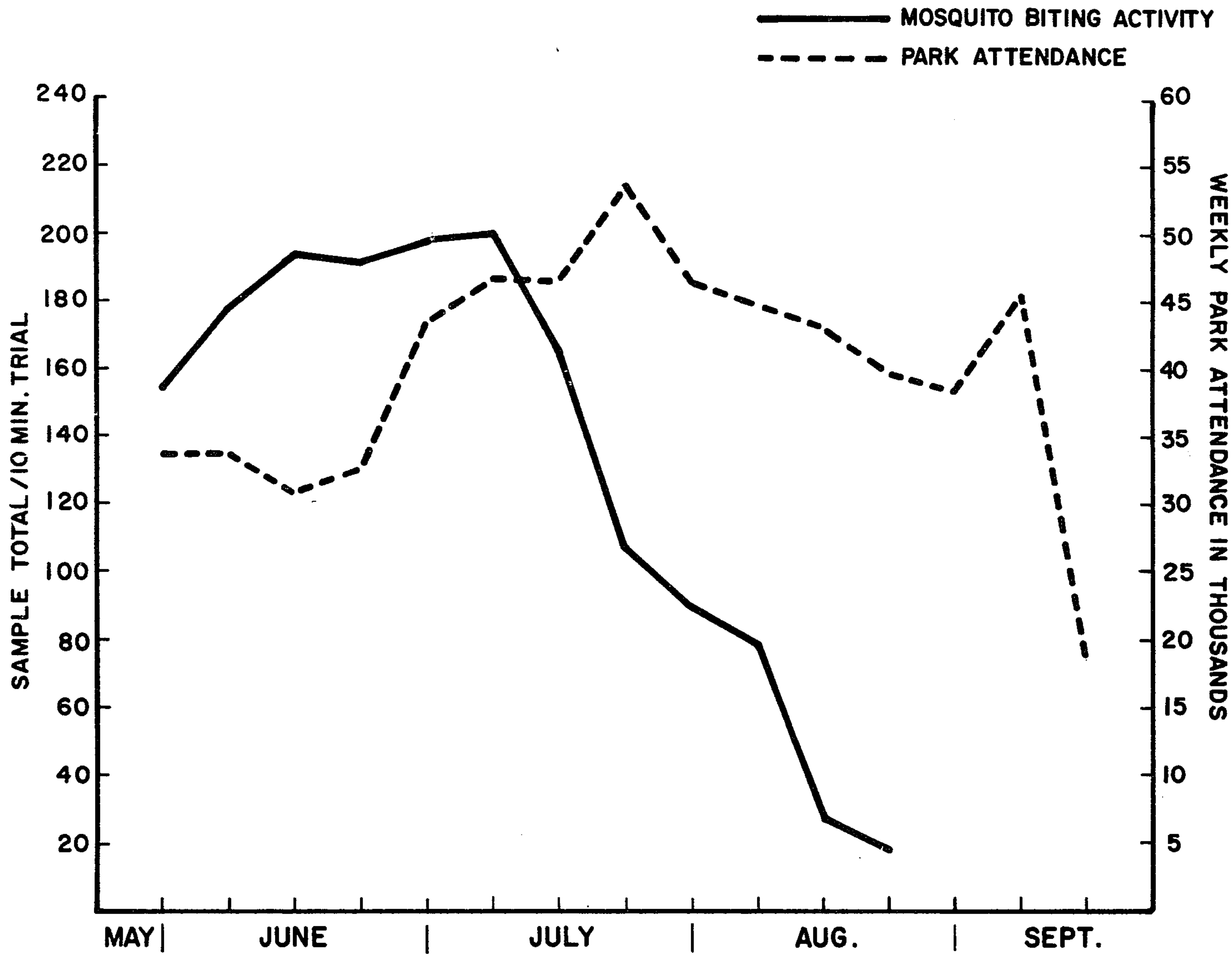

MOSQUITO BITING ACTIVITY
PARK ATTENDANCE
SAMPLE TOTAL/10 MIN. TRIAL
240
220
200
180
160
140
120
100
80
60
40
20
WEEKLY PARK ATTENDANCE IN THOUSANDS
60
55
50
45
40
35
30
25
20
15
10
5
MAY
JUNE
JULY
AUG.
SEPT.

Figure 4

PART II

A SYSTEMS SCIENCE APPROACH TO THE STUDY OF BITING INSECT POPULATIONS IN MICHIGAN STATE PARKS[1]

INTRODUCTION

A previous survey has established that species of the A. stimulans and A. communis complexes are largely responsible for biting insect problems in Michigan state parks. These mosquitoes are the woodland variety and utilize temporary lentic pools as breeding sites. These pools are formed as a result of snow melt and flooding conditions prevalent in forested areas during early spring. Due to the importance of the woodland Aedes group as potential disease vectors and nuisances in the park system, a study was undertaken to clearly define the relationship between the aquatic environment and the immature life stages. A systems science approach was used to provide an operational framework to determine what biological and aquatic features were needed for this study. Additional benefits that would be gained from this approach are identification of specific data requirements and research priorities necessary in a well-coordinated biological study.

The first step in constructing this systems model was selecting model components and adequate state variables to represent them, a process known as aggregation (Patten, 1972). The Aedes life cycle and the respective aquatic breeding sites are viewed, for the purposes of this study, as a collection of interacting components. When one set of components is chosen for a particular model, the robustness of the real system is lost. This was the difficulty encountered when the initial choice of components and behavioral features for the Aedes ecosystem was made. As a result, reliance on previous biological information and data was necessary in structuring the Aedes system model to obtain a reasonable facsimile of the natural ecosystem.

DEFINITION OF THE *AEDES* ECOSYSTEM

The modeling process was concerned with those univoltine *Aedes* mosquitoes that utilize temporary lentic pools as developmental sites for the immature life stages. Upon emergence from these aquatic areas, the adults assume a terrestrial existence for the remainder of their life span. Since a system may be defined as a collection of objects, each behaving in such a way as to maintain behavioral consistency with its environment as well as objects in the system, the life cycle and environmental interactions of this group of *Aedes* mosquitoes were partitioned into a conceptualized ecosystem (Caswell et al., 1972). As a result the various phases of mosquito development became a life system with instar and adult stages represented by specific components. The expression of this phenomenon as a structured diagram is shown in Fig. 1. Essentially, it represents a population flow chart with life components coupled to physical components representing the woodland pool.[2] Components that interact exclusively with the woodland pool are the spring egg Ψ_4 and immature $\Psi_{5,j}$ stages while the adult Ψ_6 and summer egg Ψ_7 stages are placed in a position of interaction with the terrestrial environment.[3] Those components representing the aquatic environment are the dissolved oxygen concentration Ψ_1, water temperature Ψ_2, and water depth Ψ_3 of the woodland pool. They were chosen from an infinite array of aquatic parameters as key factors in the response of the spring egg and immature stages.

Because a physiological reorganization occurs between the summer egg Ψ_7 and spring egg Ψ_4 components and no attempt was made to model these physiological states (diapause, conditioning, reactivation), a break designated as overwintering delay is positioned at this point in the system. During this time a changed physiological state and environment are mandatory for the continued functioning of the system. The two $\Psi_{5,5}$ components designating the pupal stage serve to separate the population according to sex. Since final adult differentiation is realized during this stage, a definitive sex ratio results at the time of emergence. That portion of population designated as the adult female component Ψ_{6F} will have direct input into the aquatic environment while the adult male component Ψ_{6M} is perceived as an end point in the system.

The next step in this sequential structuring process was to describe the behavior of the components. A behavioral description specifies an object's overall behavior through time in terms of behavioral features selected by the observer. At any point in time, the behavior of a component in the *Aedes* system is specified as the values assumed by a set of behavioral features (i.e., stimuli and responses). The choice of behavioral characteristics as well as the components of the *Aedes* ecosystem was initially made from a vast array of features on the basis of knowledge accumulated by the author. Construction of the model was aided by a review of entomological journals supplemented by the studies conducted in Michigan state parks. Since the primary goal was to study immature-aquatic interaction, emphasis was placed on those behavioral features that described the behavior of this portion of the ecosystem. With these concepts taken into consideration, the diagram shown in Fig. 1 was broken down into its separate components for the purpose of individual study. This set and their respective behavioral features are shown in Table 1.

Orientation of Behavioral Features into a Stimulus and Response Set

Once the set of behavioral features was selected, they were oriented into a stimulus-response set. By joining the components at their points of interaction a system graph was constructed (Fig. 2). At the points of interconnection the behavioral features are perceived as responses (determined within a component) or stimuli (determined at the interconnection or outside the system). These two configurations are represented in Fig. 2 by the general form notation Rb_i and Sb_i, respectively. The behavioral features oriented as stimuli to the aquatic environment components Ψ_1 - Ψ_3 are (with the exception of water temp Sb_1) determined outside the system and were viewed as external stimuli to the *Aedes* system. The aquatic component Ψ_1 representing dissolved oxygen interacts exclusively with the spring egg stage Ψ_4 while the components for water temperature and level, Ψ_2 and Ψ_3, interact with the immature life stages, $\Psi_{5,j}$. It should be re-emphasized that because a precise description of aquatic-immature interaction was required, a component $\Psi_{5,j}$ was needed to represent each of the five stages of the immature portion of the life cycle.

To view the immature component as having no internal structure resulted in the invalid assumption that the aquatic stimuli affect all immature stages equally. The response variables of the spring egg and larval stages were a function of the stimuli they receive from the aquatic components and of their state variables. In Fig. 2, the populations in various life stages were designated as state variables and adequately described the internal structure of the population.

Since we were interested primarily in control of aquatic life stages and since the adult and summer egg stage were interacting only with the terrestrial environment, we did not model in detail the behavior of these life stages. While the occurrence of terrestrial interactions cannot be questioned, these components were not seen as interacting with the aquatic environment, and the exclusion of external terrestrial stimuli will not affect the adequacy of the proposed simulation. In representing the internal behavior of egg input by the adult Ψ_{6F} stage, Rb_{13} was viewed as occurring at 24 one-inch levels along the sides of the pool. These individual gradients are designated as the area in which eggs are positioned for eventual spring flooding, controlled by the hatching stimulus Sb_8 (water depth). Thus the summer egg Ψ_7 and spring egg Ψ_4 are viewed as sets of 24 variables arranged as a column vector.

Construction of Free Body Models

The next step in this approach was the construction of free body models in isolation from other parts of the system. The breaking of the system's components into free body form was required due to the sheer complexity of the Aedes ecosystem. In essence, free body models prohibit making the behavior of one component a direct function of the behavior of another component. The free body model of a component is a set of functions which specifies the values for the responses and state variables based on the stimuli presented and the state of the system (which retains information about the stimulus history of the object). Fig. 3 diagrams the components of the Aedes system in free body form and Table 2 lists the free body equation forms of these models. The state and response equations take the following general form.

$$\frac{d}{dt} \Psi_i = F_i \ (\Psi_i, S_i, t)$$

$$R_i = G_i \ (\Psi_i, S_i, t) \qquad \text{(Caswell et al., 1972)}$$

The free body models for the first instar and pupal stages were constructed separately as each possesses a behavioral feature (maturation to first instar Sb_{10} and emergence to adult Rb_{12}) not possessed by the others. The rest of the immature stages $\Psi_{5,j}$ (j = 2, 3, 4) have identical behavioral sets and are modeled identically (but with different parameter values). As component Ψ_{6M} was viewed as an end point in the system, no response equation is generated. It is for the simultaneous solution of series of equations of this general form that a computer simulation of the Aedes model was constructed.

A discussion of actual free body model equations used in the computer program is beyond the scope of this paper. However, two examples are briefly described in the discrete-time form used in the simulation. The dynamics of the component water depth Ψ_3 is expressed and updated in the following state and response equations:

$$\Psi_3(t+1) = [\Psi_3(t) + (Sb_2)(Sb_9)(AREAF) - Sb_7]\ [0.95 + 0.05\ (Sb_9)]$$

$$Rb_8(t) = \Psi_3(t)$$

where $Sb_9 = 0.9 - 0.01$ (DAY). Runoff fraction Sb_9 into the pool was computed from a linear approximation of data obtained from the National Weather Service for average runoff proportion (i.e., 1 - proportion absorbed) in Michigan during the months of March through June. It was multiplied by an area factor (AREAF) of 10 to represent approximate ratio of microbasin area to surface area of the pool.[4] (Currently a time lag of one day for 0.5 of the runoff from a day's precipitation has been added to the computer simulation.) The term $[0.95 + 0.05(SB_9)]$ represents the calculation of the proportion of water not absorbed into the ground and was our rough estimate, pending results of subsequent studies. Precipitation Sb_2 and evaporation Sb_7 are daily inputs into the simulation model and were obtained from data supplied by the National Weather Service at Michigan State University.

The biological components were much more difficult to model due to their complexity and lack of information on many of the specific behavioral mechanisms. Therefore results of experimental work conducted on <u>Aedes</u> physiology were initially incorporated into portions of the simulation equations. The life stage discussed is the spring egg component $\overline{\Psi}_4$, a vector of 24 one-inch levels representing egg position along the flood line of a woodland pool. Since a break in the system occurs between components $\overline{\Psi}_7$ and $\overline{\Psi}_4$, a transfer of last year's viable eggs from $\overline{\Psi}_7$ to $\overline{\Psi}_4$ is accomplished by the simulation at the beginning of the current season. Whenever the water temperature Sb_1 is > 5° C and dissolved oxygen concentration is < 8 ppm hatching may occur. Other conditions for egg hatch are:

FDO > PDO	hatch = 0
FDO = PDO	continue started hatch but do not initiate new hatch
FDO < PDO	continue started hatch and initiate new hatch

where (FDO) and (PDO) are the current and previous day's dissolved oxygen concentration, respectively. When hatching is determined to be possible, the state equation for each submerged gradient level i (i.e., $i < Sb_8 + 0.5$ where the addition of 0.5 allows a gradient one-half to completely flooded to be designated as submerged) must be recalculated as follows:

$$\Psi_{4,i}(t+1) = \Psi_{4,i}(t)(0.5)$$

To simulate delayed hatching effect, half of the eggs are carried over to the next day while the remainder either hatch or become non-viable according to the response equation:

$$Rb_{10,i}(t) = [\Psi_{4,i}(t)]\,[(1 - 0.1225(Sb_3)]\ 0.5$$

The term $[1 - 0.1225\ (Sb_3)]$ is a linear approximation expressing the percentage of eggs that will hatch as a function of dissolved oxygen Sb_3 (Judson, 1960). When hatching conditions are not met the state and response equations take the following form:

$$\overline{\Psi}_4(t+1) = \overline{\Psi}_4(t)$$

$$Rb_{10}(t) = 0$$

The total egg hatch in the woodland pool is determined by summing $Rb_{10,i}(t)$ over all submerged egg containing gradients, i.e., if $NG = \text{Min}\ (24,\ Sb_8 + 0.5)$

$$Rb_{10}(t) = \sum_{i=1}^{NG} Rb_{10,i}(t)$$

These, then, are examples of actual free body equations constructed for two components of the <u>Aedes</u> system. The procedure is repeated for all components (Ψ_1, Ψ_2, and $\Psi_5 - \Psi_7$) with the resultant equations being utilized in the computer simulation model to describe the dynamics of the <u>Aedes</u> life system.

Footnotes

[1]Journal Article No. 6804 Michigan Agricultural Experiment Station. This research was supported by a fellowship grant from the Michigan State Department of Natural Resources.

[2]Associated with each component i is a state variable Ψ_i. The variable $\Psi_i(t)$ describes the state of the component at time t, and its value is continually updated as a function of the component's state and stimuli at time t. The state variable often represents an accumulation of material, energy, or organisms at some point in the system, and instances of each of these uses are found in this model.

[3]The determination of immature-aquatic interactions can be deduced on the basis of a single life component Ψ_5 as all immature stages are interacting with identical aquatic features. However, the responses to these features are not identical and it was necessary to generate five distinct state and response equations. Hence the $\Psi_{5,j}$ $(j = 1, 2, 3, 4, 5)$ designation was used to indicate instar and pupal responses.

[4](Variable names) used throughout this portion of the paper are the actual variable names utilized in the computer program.

Table 1. Behavioral features associated with components of <u>Aedes</u> ecosystem with emphasis on immature-aquatic interactions

Component		Behavioral Features	
Ψ_1	Dissolved Oxygen	b_1	H_2O Temp.
		b_2	Precip.
		b_3	DO_2
Ψ_2	Water Temperature	b_1	H_2O Temp.
		b_4	Air Temp. (Max. & Min.)
		b_5	Radiation
		b_6	Soil Temp.
Ψ_3	Water Depth	b_2	Precip.
		b_7	Evap.
		b_8	H_2O Depth
		b_9	Runoff
Ψ_4	Spring Egg Stage	b_1	H_2O Temp.
		b_3	DO_2
		b_8	H_2O Level
		b_{10}	Maturation to 1st Instar
		b_{14}	Egg Overwinter
$\Psi_{5,j}$	Immature Stages $j = 1, 2, 3, 4, 5$	b_1	H_2O Temp.
		b_8	H_2O Level
		b_{10}	Maturation to 1st Instar
		$b_{11,j}$	Maturation from Instar j to (j + 1)
		b_{12}	Emergence to Adult
Ψ_{6F}	Female Adult Stage	b_{12}	Emergence to Adult
		b_{13}	Egg Lay
Ψ_{6M}	Male Adult Stage	b_{12}	Emergence to Adult
Ψ_7	Summer Egg Stage	b_{13}	Egg Lay
		b_{14}	Egg Overwinter

Table 2. State and response equation forms generated by the free body models of each component in the *Aedes* system

State Equation Forms	Response Equation Forms
$\frac{d}{dt}\Psi_1 = F(\Psi_1, Sb_1, Sb_2, t)$	$Rb_3 = G(\Psi_1, Sb_1, Sb_2, t)$
$\frac{d}{dt}\Psi_2 = F(\Psi_2, Sb_4, Sb_5, Sb_6, t)$	$Rb_1 = G(\Psi_2, Sb_4, Sb_5, Sb_6, t)$
$\frac{d}{dt}\Psi_3 = F(\Psi_3, Sb_2, Sb_7, Sb_9, t)$	$Rb_8 = G(\Psi_3, Sb_2, Sb_7, Sb_9, t)$
$\frac{d}{dt}\Psi_{4,i} = F(\Psi_{4,i}, Sb_1, Sb_3, Sb_8, Sb_{14,i}, t)$	$Rb_{10} = G(\Psi_{4,i}, Sb_1, Sb_3, Sb_8, Sb_{14,i}, t)$
$i = 1, 2, \ldots 24$	$i = 1, 2, \ldots 24$
$\frac{d}{dt}\Psi_{5,1} = F(\Psi_{5,1}, Sb_1, Sb_8, Sb_{10}, t)$	$Rb_{11,1} = G(\Psi_{5,1}, Sb_1, Sb_8, Sb_{10}, t)$
$\frac{d}{dt}\Psi_{5,j} = F(\Psi_{5,j}, Sb_1, Sb_8, Sb_{11,j-1}, t)$	$Rb_{11,j} = G(\Psi_{5,j}, Sb_1, Sb_8, Sb_{11,j-1}, t)$
$j = 2, 3, 4$	$j = 2, 3, 4$
*$\frac{d}{dt}\Psi_{5,5F} = F(\Psi_{5,5}, Sb_1, Sb_8, Sb_{11,4}, t)$	$Rb_{12} = G(\Psi_{5,5}, Sb_1, Sb_8, Sb_{11,4}, t)$
$\frac{d}{dt}\Psi_{6F} = F(\Psi_{6F}, Sb_{12}, t)$	$Rb_{13} = G(\Psi_{6F}, Sb_{12}, t)$
$\frac{d}{dt}\Psi_{6M} = F(\Psi_{6M}, Sb_{12}, t)$	
$\frac{d}{dt}\Psi_{7,i} = F(\Psi_{7,i}, Sb_{13,i}, t)$	$Rb_{14,i} = G(\Psi_{7,i}, Sb_{13,i}, t)$
$i = 1, 2, \ldots 24$	$i = 1, 2, \ldots 24$

*Identical equation for $\Psi_{5,5M}$.

Fig. 1. A diagram of woodland Aedes population components and their respective environments. Components Ψ_1, Ψ_2, Ψ_3, represent dissolved oxygen concentration, water temperature, and water depth of woodland pool, respectively. Component Ψ_4, spring egg stage. Component $\Psi_{5,j}$ (j = 1, 2, 3, 4, 5); 4 larval instars and pupil stages where $\Psi_{5,5}$ is subdivided into a male and female set. Component Ψ_6; adult stage subdivided into a male and female set. Component Ψ_7, summer egg stage.

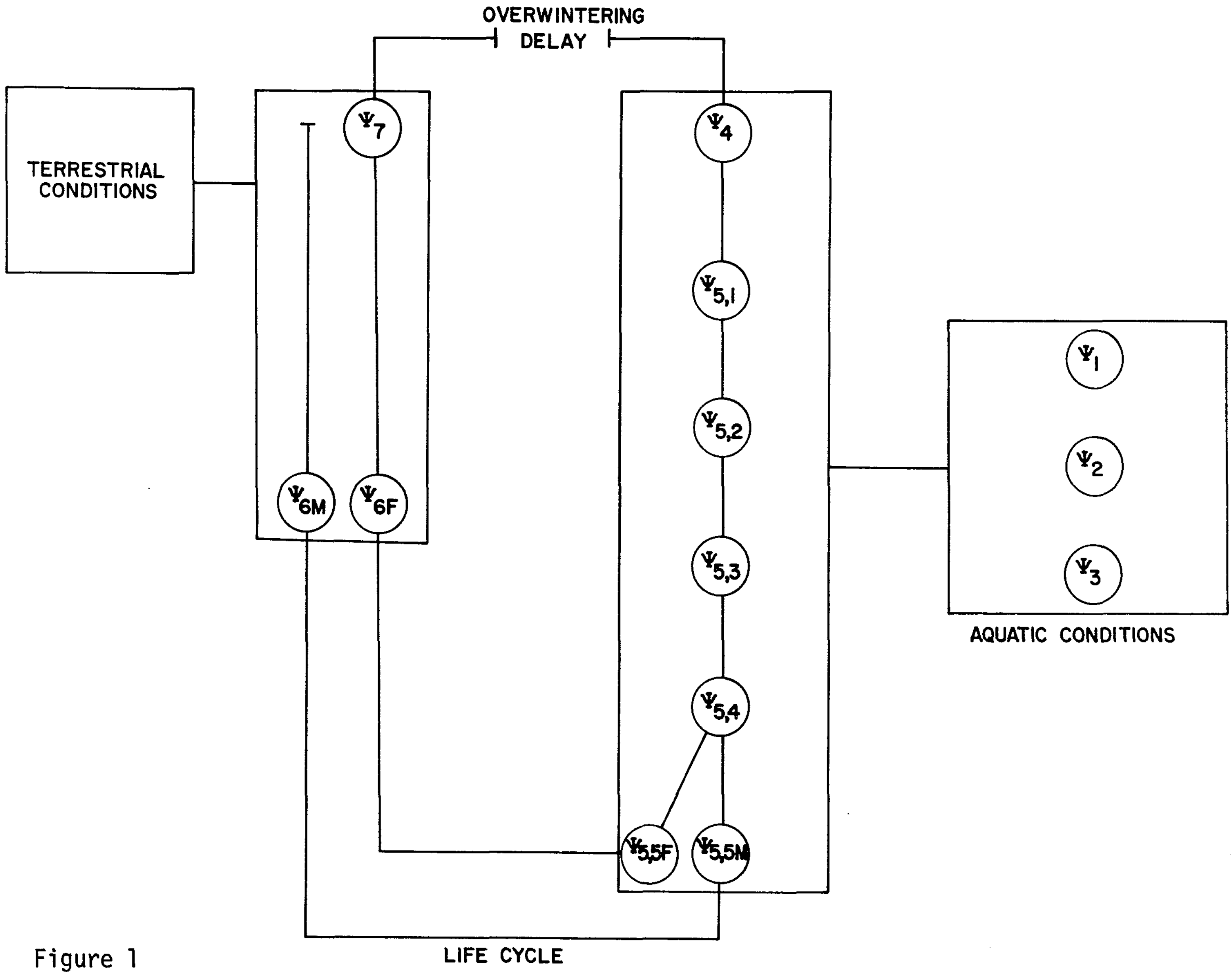

OVERWINTERING
DELAY
TERRESTRIAL CONDITIONS
Ψ_7
Ψ_{6M}
Ψ_{6F}
Ψ_4
$\Psi_{5,1}$
$\Psi_{5,2}$
$\Psi_{5,3}$
$\Psi_{5,4}$
$\Psi_{5,5F}$
$\Psi_{5,5M}$
Ψ_1
Ψ_2
Ψ_3
AQUATIC CONDITIONS
LIFE CYCLE

Figure 1

Fig. 2. System graph of *Aedes* mosquito ecosystem indicating stimulus Sb_i and response Rb_i orientation of the behavioral features.

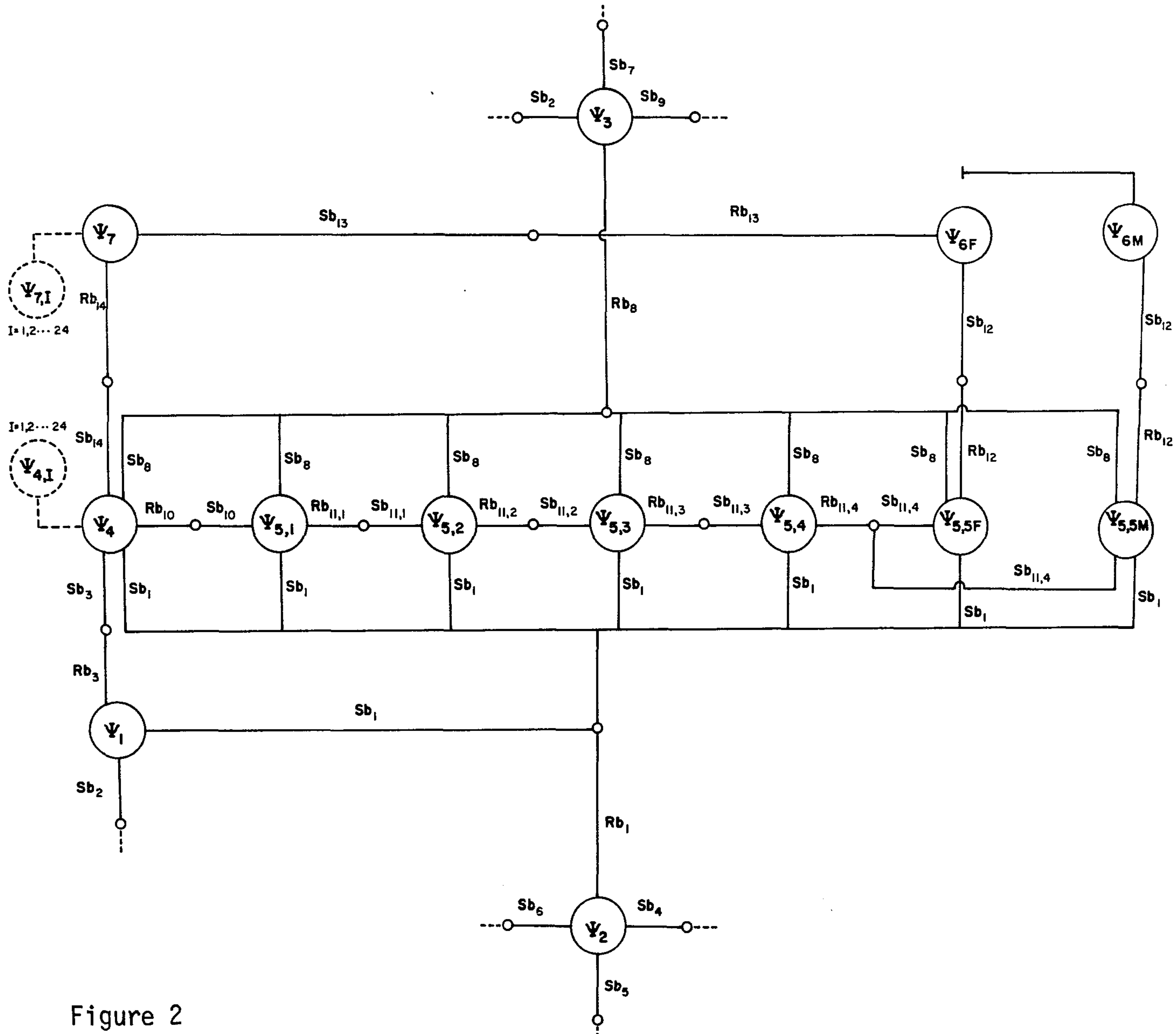

Sb_7
Sb_2
Ψ_3
Sb_9
Ψ_7
Sb_{13}
Rb_{13}
Ψ_{6F}
Ψ_{6M}
$\Psi_{7,I}$
Rb_{14}
I=1,2 ··· 24
Rb_8
Sb_{12}
Sb_{12}
I=1,2 ··· 24
Sb_{14}
$\Psi_{4,I}$
Sb_8
Sb_8
Sb_8
Sb_8
Sb_8
Sb_8
Rb_{12}
Sb_8
Rb_{12}
Ψ_4
Rb_{10}
Sb_{10}
$\Psi_{5,1}$
$Rb_{11,1}$
$Sb_{11,1}$
$\Psi_{5,2}$
$Rb_{11,2}$
$Sb_{11,2}$
$\Psi_{5,3}$
$Rb_{11,3}$
$Sb_{11,3}$
$\Psi_{5,4}$
$Rb_{11,4}$
$Sb_{11,4}$
$\Psi_{5,5F}$
$\Psi_{5,5M}$
Sb_3
Sb_1
Sb_1
Sb_1
Sb_1
Sb_1
$Sb_{11,4}$
Sb_1
Sb_1
Rb_3
Ψ_1
Sb_1
Sb_2
Rb_1
Sb_6
Ψ_2
Sb_4
Sb_5

Figure 2

Fig. 3. Construction of free body models associated with the *Aedes* components.

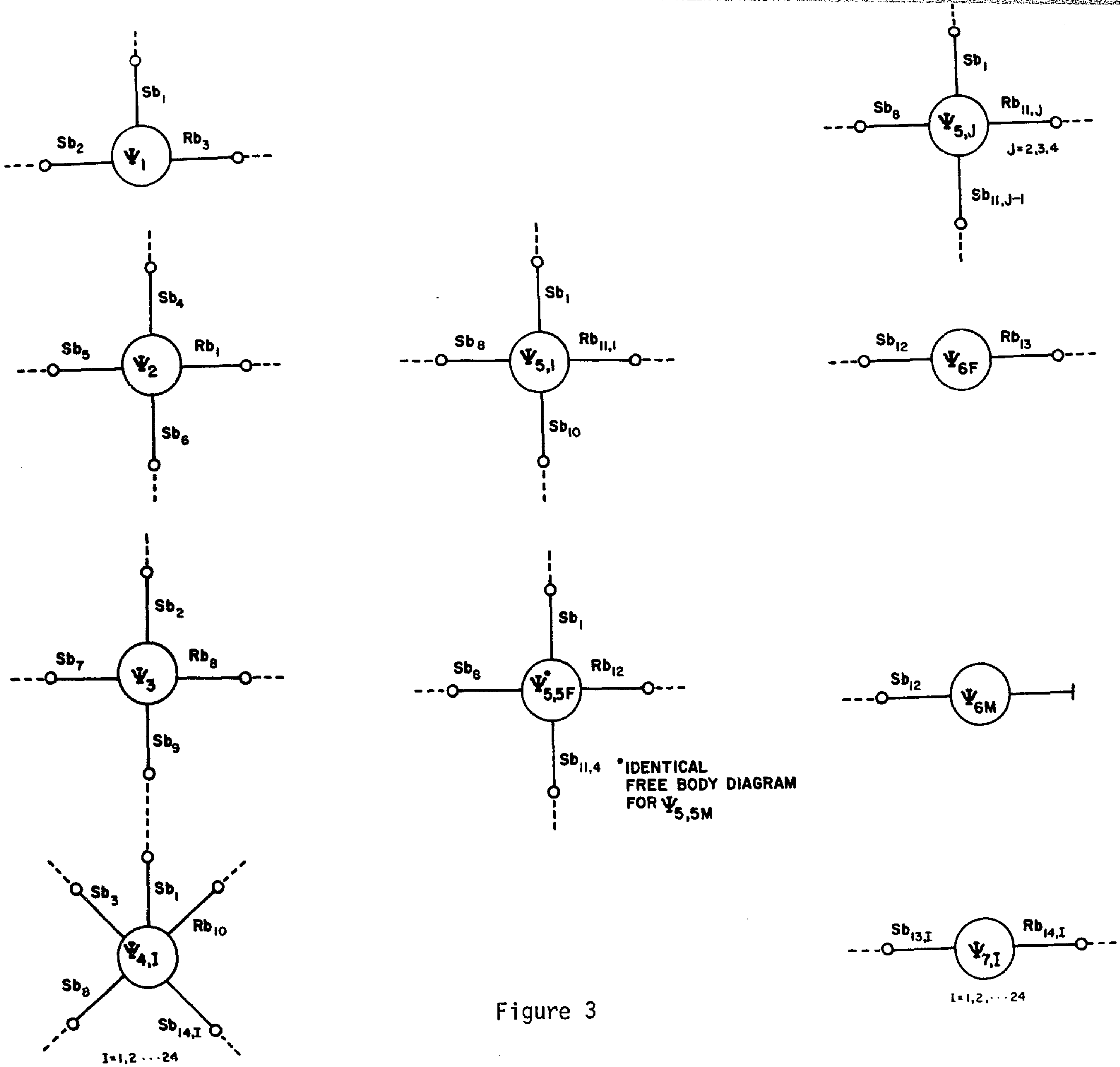

Sb1
Sb2
Rb3
Ψ1
Sb4
Sb5
Rb1
Ψ2
Sb6
Sb2
Sb7
Rb8
Ψ3
Sb9
Sb3
Sb1
Rb10
Ψ4,I
Sb8
Sb14,I
I=1,2 ···24
Sb1
Sb8
Rb11,1
Ψ5,1
Sb10
Sb1
Sb8
Rb12
Ψ*5,5F
Sb11,4
*IDENTICAL
FREE BODY DIAGRAM
FOR Ψ5,5M
Sb1
Sb8
Rb11,J
Ψ5,J
J=2,3,4
Sb11,J-1
Sb12
Rb13
Ψ6F
Sb12
Ψ6M
Sb13,I
Rb14,I
Ψ7,I
I=1,2,···24

Figure 3

PART III

CONSTRUCTION AND REFINEMENT OF A COMPUTER SIMULATION MODEL FOR POPULATION STUDIES OF WOODLAND POOL *AEDES* MOSQUITOES[1]

INTRODUCTION

Once a system model for Aedes woodland mosquitoes was obtained, a computer simulation was constructed to simulate the dynamics of the insect and of the woodland pool ecosystem. A computer simulation is merely one of the methods available for examining behavioral sequences and external stimuli to an ecosystem. In some instances this approach to biological studies can yield very powerful results (Caswell, 1972). However, the inherent problem in modeling ecological systems is that the assumptions necessary to achieve an analytically acceptable structure may be so gross that the results of analysis have minimum relevance to the real world. Therefore constant experimentation with the Aedes ecosystem and comparison with inherent qualities and defects of the model must be undertaken by the biologist to insure a representative simulation. The optimum approach may be a combination of analytical techniques ranging from computer simulations to numerical solution and graphical analysis. Comparison of results would give an approximation of the model's sensitivity in describing real world situations.

Equations used in the computer program were formulated with the aid of a system graph developed to study this entomological problem. Information and data utilized in the model construction were obtained from surveys conducted in Michigan state parks and an extensive literature review.

MODELING THE BIOLOGICAL COMPONENTS

As in any modeling process assumptions were made before the actual model construction began. Following are the reasoning processes underlying the equation forms used in the simulation. It was assumed that water temperature was the key factor in determining the maturation rates of immature stages. Of the various attempts to mathematically describe water temperature effect on mosquito larval growth rates (Huffaker, 1944; Lal, 1953; Haufe and Burgess, 1956; Nielsen and Evans, 1960), the catenary formula (Janisch, 1932) utilized by Huffaker (1944) was chosen for use in our simulation. The choice of this formula met the requirement of precise mathematical descriptions for individual immature stage growth rates. This was necessary because each instar and pupal stage growth rate response was different and required the generation of five distinct state and response equations. Also, the addition of a positive and negative exponential curve used in this formula (representing the acceleration of maturation rates through rising temperature and retardation during the developmental process, respectively) is preferred to expressing developmental rates as a linear function of temperature since a straight line relationship does not adequately explain insect development at the extremes of the temperature range. The actual progression of immature cohorts through the larval stages was assumed to be uniform with minimal variance of growth rates within a cohort.

Assumptions concerning the dynamics of egg hatch took into consideration the role of dissolved oxygen concentration in initiating the egg hatch response. Numerous authors have studied this phenomenon (Borg and Horsfall, 1953; Horsfall et al., 1958; Judson, 1960; Trpis and Horsfall, 1967) and have shown a decreasing gradient of dissolved oxygen was required to initiate the egg hatch response. A linear approximation of data (Judson, 1960) concerning the effect of static levels of dissolved oxygen on two species of Aedes mosquitoes was initially utilized in the simulation. The data were obtained from that portion of the experiment utilizing eggs stored at 90-100 percent relative humidity since the assumption was that eggs in a natural environment are positioned in locations that maintain a high soil moisture gradient. In the park study areas these locations are moist layers of plant detritus along the flood line of woodland pool micro-basins and are usually protected from moisture loss by a dense forest canopy. The storage of eggs in the top 24 inches of a pool area was viewed as the egg input response by the adult female population. The females are assumed to oviposit the eggs in the gradients closest to the receding water level and the point of maximum flood. This assumption agreed with Horsfall's (1963) observations concerning egg positioning of A. stimulans mosquitoes in woodland pool microbasins. All surviving adult females were assumed to have taken a blood meal needed for egg formation since the park areas support substantial populations of small mammals and are visited by thousands of campers during the summer months. The gonotrophic cycle of the woodland Aedes mosquito was assumed to occur over a seven day period with egg oviposition occurring every seventh day with each female laying an average of 70 eggs along the floodline of the woodland microbasin. These assumptions were based on observations (Barr, 1958) concerning the Aedes stimulans complex indicating that the preoviposition period was approximately seven days with a mean egg lay of 70 per female. The results of that study also indicated no appreciable delay in oviposition by females of this species complex. Finally, fertilization of the emerging females was assumed to be 100 percent. Once these assumptions were made and incorporated into the modeling process, a computer simulation of the Aedes system was attempted.

Dynamics of the Immature Stages

The most important biological component from the aspect of the modeling process was the one representing the immature life stages. The dynamics of movements of organisms within and among these stages are made by the program on a daily basis and controlled by three subroutines and a function subprogram (Fig. 1A).

The immature stages are represented in the program by a two-dimensional vector IN (i,j).[2] The first subscript refers to the number of days a population cohort has been present in a particular stage, while the second subscript refers to the various stages as follows:

a value of	refers to
1	instar 1
2	instar 2
3	instar 3
4	instar 4
5	male pupa
6	female pupa

For example, IN (12,2) contains a count of the number of larvae which have been in instar 2 for 12 days. Subroutine DEVLOP directs the development within each of these life stages. Every day, the elements of each stage are advanced within that stage to the next position, subject to a daily mortality rate (stored as a vector, KILL(j), where j takes values according to the table above). A 20 day limit has been selected as a maximum expected duration for any one stage; however, in the event that a longer progression is required, cohorts simply remain in the 20th element (once reached) until graduation to the next stage. This process is expressed by the following equations

$$\mathrm{IN}(i,j) = \begin{cases} (\mathrm{IN}(20,j) + \mathrm{IN}(19,j))*(1 - \mathrm{KILL}(j)) & \text{if } i = 20 \\ 0 & \text{if } i = 1 \\ \mathrm{IN}(i.j)*(1 - \mathrm{KILL}(j)) & \text{otherwise} \end{cases}$$

where i sequences in unit decrements from twenty to one, and j sequences in unit increments from one through six.

Subroutine GRADUAT graduates an immature cohort (group of individuals of the same maturity at a given time) to the next instar stage dependent on the rate of development calculated by subroutine GRADRAT. The latter subroutine utilizes a function subprogram CTNRY to set RATE(I); the number of days of development required before movement from one immature stage to the next can be accomplished. Function CTNRY utilizes the catenary formula which describes the duration of each larval and pupal stage and takes the following form

$$t = \frac{m}{2}\left(a^{T} + a^{-T}\right)$$

where t = time, m = developmental time at the empirically determined optimum, a = constant determining the slope of the curve, and T is the temperature in degrees above or below the optimum. Then, each day, subject to certain constraints, immature cohorts in each stage may be graduated into the succeeding stage. The first instar stage must be presented with a water temperature in excess of 8° C prior to graduation to the second instar; while the second instar requires a 15° C minimum temperature before graduating to third instar. The equation below details the accumulation of cohorts for graduation; while the table below summarizes the graduation mechanics:

$$\text{SUM for stage } j = \sum_{i=\text{RATE}(j)}^{20} 0.95*\text{IN}(i,j)$$

cohort represented by this total	is added to this location	
SUM for stage 1	IN(1,2)	second instar, day 1
SUM for stage 2	IN(1,3)	third instar, day 1
SUM for stage 3	IN(1,4)	fourth instar, day 1
½SUM for stage 4	IN(1,5)	male pupa, day 1
½SUM for stage 4	IN(1,6)	female pupa, day 1
SUM for stage 5	ADLT(1)	adult male
SUM for stage 6	ADLT(2)	adult female, day 1

As indicated in the equation above, on a given day 95 percent of the total count in each element eligible for graduation (i.e., the element represents a population which has been present in the given stage for at least the number of days indicated as the value of RATE for that stage) are accumulated into a sum and transferred into the day 1 position of the succeeding stage (the remaining 5% stay in the element, to be subject to graduation conditions on the following day). At the point of graduation from fourth instar, sex determination takes place and transfer is made into the male and female pupal stages (50% of the accumulated sum into each).

Dynamics of the Egg Stage

As there is a break in the system between the summer and spring egg components, a transfer of last year's viable eggs from the summer egg to the spring egg vector (both consisting of 24 elements representing the productive egg region of the pool) is accomplished by the simulation at the beginning of the current season. Since the response of the spring egg component is maturation to first instar (shown graphically in Fig. 1B), egg hatch may occur when the program determines that the water temperature is > 5° C and dissolved oxygen concentration is < 8 ppm. Other conditions for egg hatch are:

FDO > PDO	hatch = 0
FDO = PDO	continue started hatch but do not initiate new hatch
FDO < PDO	continue started hatch and initiate new hatch

where FDO and PDO are the current and previous day's dissolved oxygen concentration, respectively. When hatching is determined to be possible, total egg hatch is computed:

$$IN(1) = \sum_{I=ITW}^{NG} [IEGG(I)] * [1.0 - 0.1255 * FDO] * 0.5$$

According to the response equation half of the eggs are carried over to the next day (to simulate a delayed hatching effect) while the remainder either hatch as determined by [1.0 - 0.1225 * FDO] * 0.5 or become non-viable. This is a linear approximation expressing the percentage of eggs that hatch as a function of dissolved oxygen (Judson, 1960). IEGG(I) is the number of eggs in gradient I (where I = 1, 2, ... 24) and the sum to be transferred into the first instar stage (IN(1)) is accumulated from all submerged egg containing gradients, i.e., I takes values starting from the index of the topmost submerged gradient, ITW, and continuing to the value of NG (Index of the deepest egg containing gradient) by unit increments. The value of NG and the number of submerged gradients on a given day are obtained from

$$NG = Min\ (24,\ DM + 0.5)$$

$$NWET = DEEP - XSDPTH + 0.5$$

where the addition of 0.5 allows a gradient one-half to completely flooded to be designated as submerged. Since egg gradients are assumed to be restricted to the upper 24 one-inch levels, and pool maximum depth (as input variable, DM) may range up to 36 inches, XSDPTH is a measure of water depth below this productive egg region. This quantity of water is subtracted from the current pool depth (DEEP) with the resultant integer number of submerged egg gradients designated as NWET.

Dynamics of the Adult Stage

Adult dynamics as defined by the simulation are diagrammed in Figure 1C and expressed

MAL + MAL* (1.0 - KILL (7))

FEM (1) = FEM (1) + FEM (8)

FEM (D) = FEM (D-1) * (1.0 - KILL (7)) where D goes from eight to two by decrements of one

FEM (1) = 0

where MAL and FEM are the male and female portions of the population. The equations representing dynamics of the females calculate the number of individuals available for advancement through the eight word array, advances the cohort to the next position in the array subject to mortality, and sets the first position to zero in preparation for subsequent adult female input. Egg input response is computed by subroutine LAYIT for females positioned in the seventh position to simulate a seven-day gonotrophic cycle. The males simply remain in the first element position of the vector designated for that portion of the population. Both adult components are reduced by a daily mortality factor KILL (7).

The eggs laid by the females are designated as summer eggs and positioned in a vector (NEGG) of 24 elements (corresponding to one-inch levels along the floodline of the simulated woodland pool). Each day the eggs laid (totaled in IEGG) are dispersed evenly over the six gradients closest to the receding water level according to the following:

$$NEGG(I) = NEGG(I) + \begin{cases} IEGG/6 & \text{if condition 1} \\ IEGG/\text{number of dry gradients} & \text{if condition 2} \end{cases}$$

The conditions are

1. If IBD $\geq$ 6 then I = IBD - 5, IBD
2. If 0 < IBD < 6 then I = 1, IBD

where IBD equals the index of the bottom dry pool gradient.

MODELING THE PHYSICAL COMPONENTS

Modeling the physical components of the system was accomplished after consultation with individuals of the National Weather Service at Michigan State University and a review of research on mosquito larval development in woodland pool ecosystems. The water depth component was updated daily utilizing weather data from a data storage file. The equation utilized in the simulation included an area factor to represent the ratio of microbasin area to surface area of the woodland pool that was studied during 1972 and 1973. The amount of water absorbed into the ground was a rough estimate pending results of subsequent studies during this same time period. The meterological features oriented as stimuli to the water temperature components are air temperature and soil temperature. These factors were considered to have measurable effect on the aquatic environment of the Aedes system. In research conducted by Haufe and Burgess (1956) it was found that air temperature, wind chill and solar radiation were useful in a mathematical description of the relationship between meteorological factors and the daily average temperature of mosquito pools. The studies were conducted in a tundra region of subarctic Canada. Wind chill and solar radiation were not used in our model because the location of the woodland pools in dense, forested areas and depressed microbasin areas was assumed to minimize the effect of these meterological factors. While solar radiation was initially utilized as a behavioral feature to the water temperature component, the location of the aquatic microhabits allowed the parameter to be ignored in the later studies. Finally, the component for dissolved oxygen concentration was simulated with the following assumptions taken into consideration. Since initially the pool is filled with runoff from melting snow it was felt that data contained in Welch (1952) on the oxygen content of water saturated with air would provide a reasonable initial value for the oxygen content of the pool. The actual amount of oxygen diffusing to the mosquito eggs (positioned in the bottom sediment) was modeled according to information in Ruttner (1963) expressing the rate of oxygen diffusing into the sediment as a function of a constant A (eddy diffusion coefficient) and the range over which the concentration can vary. In the instance of a woodland pool ecosystem which in reality is an aquatic microbasin, the oxygen concentration is assumed to be uniform over depth. The actual mechanism for removal of oxygen from the pool was assumed to be microbial metabolism. This microbial uptake of oxygen in our model was assumed to be a function of temperature and an approximation of data from Allen (1968) was used in the model to simulate oxygen removal from the pool.

Dynamics of the Physical Components

The dynamics of water depth is expressed and updated by the simulation in the following way:

$$\text{DEPTH} = [\text{DEPTH} + \text{PRECIP} * \text{RNF} * \text{AREAF} - \text{EVAP}]\ [0.95 + 0.05 * \text{RNF}]$$

where RNF = 0.9 - 0.01*DAY. Runoff fraction, RNF, into the pool was computed from a linear approximation of data obtained from the National Weather Service for average runoff proportion (i.e., 1 - proportion absorbed) in Michigan during the months of March through June. It was multiplied by an area factor (AREAF) of 10 to represent approximate ratio of microbasin area to surface area of the pool. A time lag of one day for 0.5 of the runoff from a day's precipitation has been added to the computer simulation. The term [0.95 + 0.05*RNF] represented the calculation of the proportion of water not absorbed into the ground and was our rough estimate, pending results of subsequent studies. Precipitation (PRECIP) and evaporation (EVAP) are daily inputs into the simulation model and were obtained from data supplied by the National Weather Service at Michigan State University.

The dynamics of the component water temperature is expressed and updated by the program in subroutine WATERT. Once the routine determined that there was water present in the pool, the average water temperature for a 24-hour period was calculated based on the number of six inch water gradients present in a 36 inch maximum depth woodland pool (numbered from the bottom up). The previous day's average temperature (TW) is set in all water gradients expressed as a six element vector, T1. Input variables are evaporation, precipitation, and water depth computed by a call to subroutine WATER. The number (IX) of six inch gradients filled with water was then calculated and the average temperature determined by the following formulas where TA and TS equal air and soil temperature, respectively, and M goes from IX-1 to 2 by decrements of 1:

$$WT = (T1(1) + TA + TS*2)/4 \qquad \text{If } IX \leq 1$$

$$T1(IX) = TA + TW/2$$
$$T1(M) = [T1(M+1) + T1(M-1)]/2 \qquad \text{If } IX > 1$$
$$T1(1) = (T1(2) + 2*TS)/3$$

The first condition states that if the number of water filled gradients is less or equal to one then the water temperature is equal to an average of the water gradient, air, and soil temperatures. The second condition states that if the number of water filled gradients is greater than 1, the top level is an average of the air and water temperature while each subsequent gradient (with exception of bottom gradient) is the average of the one above and below it. The bottom gradient is the average of the soil temperature and the second gradient to the bottom. In both conditions 1 and 2 the soil temperature is weighted by a factor of 2. Finally the average water temperature is weighted by volume of each gradient

$$TW = AH/AV$$

where AH equals the total of volume X temperature for each gradient and AV equals the total of volumes for the gradients.

The component for the dissolved oxygen concentration of the woodland pool is calculated and updated in the following manner. An upper limit in parts per million of oxygen in the pool is calculated as a function of water temperature

$$PPM = MIN\ [14.0,\ 14.01 - 0.242*WTEMP]$$

where the term [14.01 - 0.242*WTEMP] was an approximation of data in Welch (1948) on the oxygen content of water saturated with air at normal pressure. The daily dissolved oxygen level is set at these values for saturation on days when precipitation occurs or on days when this value produces a decrease in dissolved oxygen. The response variable FDO representing the level of oxygen accessible to Aedes eggs in the bottom sediment is calculated as follows:

$$SAT = 0.6*DOC$$

$$UPT = [0.21 + 0.25*WTEMP]\ [12/1000]$$

$$FDO = SAT - UPT$$

The first equation represented the rate of oxygen diffusion in μg liter^{-1} hour^{-1} into the sediment of the woodland pool. The factor 0.6 is the eddy diffusion coefficient of Ruttner (1963) while DOC is the current dissolved oxygen concentration in the water. The second equation represented an approximation of oxygen uptake in μg liter^{-1} hour^{-1} by microbial activity (Allen, 1968) multiplied by a factor of 12 (to indicate our estimate of the higher bacterial activity of a lentic, depositional pool as opposed to Allen's work conducted in a lake system) and converted to parts per million. The final dissolved oxygen concentration available to the eggs (FDO) is found by subtracting the value for UPT from SAT.

This completes the discussion of the computer program structure utilized in the description of the dynamics of the Aedes system. However, a description of pool geometry was needed by the simulation to store the volume of water contained in the pool and compute the number of one-inch gradients available for egg input and hatch [Min (24, integer (max. water))]. The woodland pool microbasin is viewed as a segment from a large sphere that is depressed from the surrounding land mass. The subroutine PONDIM computes the radius of this segment according to the following formula where input variables are surface area (SURFAR) and water depth (DPTH) of the pool at maximum flood level:

$$R = (\text{SURFAR**2} + \text{DPTH**2})/(\text{2*DPTH})$$ [3]

The pool is then divided into six-inch gradients from the bottom up and the water volume stored in VOL(I) (where I = 1, 2, ... 6) according to the following segment volume formula where R is the radius of the sphere as calculated from the following equation:

$$SV = \frac{1}{3} * \pi * \text{DEPTH} ** 2 * (3 * R - \text{DEPTH})$$

PROGRAM STRUCTURE

The overall program structure for the Aedes simulation just discussed is diagrammed in Fig. 2. To provide flexibility, a modular format was utilized that would accommodate additional variables and replacement or modification of the original equations used in the system.

The mosquito's life cycle is traced by the simulation in a daily progression initialized in the egg stage and developed through the immature stages until emergence as adults. The adult stage is then followed until expiration of all adult mosquitoes with female egg deposition occurring during the adult cycle. When all eggs have hatched or become non-viable (due to environmental factors) and all of the other stages are empty, the winterizing phase established conditions for the next year's progression. The program also provides for additional years of simulation for long-term studies. The input variables for the computer simulation in two data files, WEATH and RUNDAT. The former is a weather file containing data obtained from the National Weather Service at Michigan State University. Currently air temperature (max and min), soil temperature, precipitation, evaporation, and runoff are being stored and updated on a daily basis for the months of March through August. These variables allow for the computation of values for the three physical components of the Aedes system; water temperature, water depth, and dissolved oxygen concentration of the woodland pool. The RUNDAT file contains data necessary to begin a program execution and contains information pertaining to egg lay and woodland pool conditions. Within each of the stages of development the inputs from the two files control such processes as growth and maturation rates, environmental mortality, egg viability, and sex determination in the pupal stage.

REFINEMENT OF THE MODEL'S BIOLOGICAL COMPONENTS

Immature and Adult Mortalities Used in Model

The biological information on A. stimulans-fitchii mosquitoes was implemented into the computer simulation model in order to refine the dynamics of the biological components of the Aedes system. Immature mortality rates of age intervals 7-28 are adequate estimations of larval mortalities with late instar mortality approximately 0.50. However, it was necessary to eliminate certain cohorts during the first age interval as serial egg hatch (caused by additional flooding of the woodland pool) introduced first instars into the larval population resulting in an underestimation of mortality rates. This was especially true in 1973 when the 335 count for instar I at the second sampling trial consisted entirely of newly hatched immatures and occurred after the depth of the pool went from 18 inches to a maximum flood of 36 inches. The elimination of this cohort from the life table resulted in more realistic mortality values for implementation into the model. These values are shown in the following table:

Sampling Trial	Instar Population I	II	III	Total
1	94	41	2	137
		94	9	103

which gives a mortality rate of 0.248 (survival rate 0.752). A similar procedure was utilized for data collected in 1972 when 30 first instars were collected during the second sampling trial and consisted of nine newly hatched immatures. When these individuals were eliminated a mortality rate of 0.230 (survival rate 0.770) was obtained. The revised totals are shown in the following table:

Sampling Trial	Instar Population I	II	III	Total
1	26	35		61
2	21	14	12	47

These values indicated that early development mortality was approximately 0.25 for both years. Inspection of immature life tables indicated that mortality occurred primarily during transition from one instar stage to the next. Although some daily mortality is indicated, the data does not allow an adequate separation of daily mortality effects. Survival rates used in the computer simulation are as follows:

Daily Survival	0.99	KILL(I) = 0.01
Transition Survival		
From instar I to II	0.75	
From instar II to III	0.75	
From instar III to IV	0.50	
From instar IV to pupae	0.75	
From pupae to adults	0.50	

and constitute an addition to subroutine GRADUAT. Although pupal to adult survival has no basis in the data, it was estimated to be at least 0.50. This was indicated by the field studies that showed highest mortality occurred in later instars. In addition, empirical observations indicated that substantial numbers of adult mosquitoes failed to completely emerge from their pupal cases.

Adult female mortality rates used by the simulation were calculated using data in Table 7. In the model, day of emergence is considered to be the day when the largest transition from pupa to adult takes place. Complete survival of the adult female population is insured by the model for 36 days after emergence. Thereafter rates for age intervals 36-85 in 1972 and 1973 were used to plot a composite survivorship curve (Fig. 3) that established the female survival rates utilized in the simulation. The curve was plotted after visually smoothing data for age intervals 36-64 to compensate for a divergent anomaly interpreted as due to external effects such as predation, parasitism, or environmental stress. This resulted in a daily survival rate of 0.965 (KILL(7) = 0.035). A daily rate of 0.860 (KILL(7) = 0.140) was established for age interval 64 to 71 with the population decreased in the remaining two intervals by a fixed number (1/14 of the population at the start of the interval) until mortality was 1.00. As empirical observations indicated that adult males were present for approximately two weeks after initial emergence, they were retained in the model for 14 days at which time mortality will be 1.00.

Female Gonotrophic Cycle

Refinement of the computer model in light of acquired field data required us to review literature references in search of alternative descriptions of individual biological components. In the case of female gonotrophic cycles for univoltine, early spring Aedes mosquitoes, Detinova (1968) listed results of studies by Shlenova and Bey-Bienko (1962) showing the percentage of gonotrophic cycles completed by A. communis (closely related to A. stimulans-fitchii) during one season. Table 1 is derived from that study and shows that approximately 0.3 of successive surviving portions of the female population will lay eggs on a weekly basis from the third week in June until the month of August. Utilization of this information in the simulation resulted in a weekly egg input response expressed

$$IEGG = (ADULTF * 0.3 * 70.7)$$

where IEGG = total number of laid eggs, ADULTF = total number of adult females, 0.3 = proportion of females undergoing an egg input response, and 70.7 = size of egg batch/female mosquito. For the purposes of the simulation, it was not important whether this egg input was from the first or succeeding gonotrophic cycles nor was it likely to have a detrimental effect to have all oviposition occur on one day of each week. For these reasons, the current version of the simulation will use a single variable location to represent the adult female component. Other factors relating to size of egg batch will remain unchanged.

The decision to incorporate a new procedure for simulating female gonotrophic cycles necessitated a revision of assumptions regarding geographic distribution of egg batches in the woodland pool. If the egg lay procedure previously mentioned was retained, the low level of water at the time of egg lay would have resulted in most of the eggs being deposited in gradients 18-24. This was not supported by field surveys conducted in 1972 and 1973 which indicated substantial egg hatch when gradients 6-18 were flooded. Serial egg hatch was confirmed from field studies where the appearance of newly hatched first instar larvae was observed immediately after inundation of additional surface area of the microbasin. Also, the amount and location of the egg hatch observed at the study site confirmed published observations that A. stimulans eggs are generally laid in a regular distribution across soil gradients in a region below the maximum flood line to a depth of 24 inches (Horsfall, 1973). In 1973 no larvae were present in water samples taken when only the deepest portion of the microbasin was flooded (3 to 6 inch depth); so, for the model, an assumption was made that the female utilizes an oviposition site that is moist but not submerged (hence avoidance of the pool bottom which remains flooded the longest) and all except the top six inches of soil remain sufficiently moist to be used for oviposition sites. Thus, in the simulation the female oviposits the eggs as a regular distribution in the six to twenty-four inch gradients with the top six inches receiving 0.10 of the total egg lay.

REFINEMENT OF PHYSICAL COMPONENTS

In order to refine the computer simulation's description of those aquatic parameters used as key factors in immature mosquito dynamics, periodic measurements were conducted in 1973 on maximum and minimum water temperatures, water depth, and dissolved oxygen concentration. These measurements were taken during a 14 week period beginning March 1 and continuing through June 15 at the woodland pool study area. In addition, daily measurements for meterological features oriented as stimuli to the physical components of the *Aedes* system (max-min air temp., soil temp., precipitation, and evaporation) were obtained at the aquatic microhabitat during the same time period. The data was placed on a storage file for subsequent statistical analysis and use in the refinement of the model.

Water Temperature

Analysis of meterological data showed that maximum water temperature had more influence on dissolved oxygen concentration than minimum water temperature (Table 2). It is also known from Haufe's research (1957) that immature stages of a related species have a temperature preferendum in a woodland pool ecosystem and will seek optimum temperature levels. Finally when the temperature averaging method was used to predict water temperature (version 2 of the *Aedes* simulation), larval development lagged behind the rate observed in field studies with the result that the immature population died before any of the late instar stages were reached. It was due to these three reasons that maximum water temperature was used in place of the temperature averaging method. A multiple regression analysis was conducted on the field data to determine the best relationship between maximum water temperature and a corresponding set of independent variables with the following result:

$$\text{MAXW} = [-2.5215 + (0.8812*\text{MAXAIR}) - (0.0228*\text{MINAIR}) - (0.0897*\text{SOILT}) + (0.2710*\text{YMAXW})]$$

where MAXW = maximum water temperature, MAXAIR = maximum air temperature, MINAIR = minimum air temperature, SOILT = soil temperature, and YMAXW = the previous day's maximum water temperature. The proportion of variation explained by these coefficients is 0.9520 with MAXAIR contributing almost 0.50 to the overall correlation coefficient.

Dissolved Oxygen Concentration

Dissolved oxygen concentration and various combinations of measured temperatures were analyzed by step-wise multiple regression to choose the best model in an attempt to refine the computer simulation. A comparison between measured and simulated oxygen levels indicated that the simulation was producing values in excess of actual concentrations obtained in the field. The most accurate prediction equation which emerged from the data analysis was as follows:

$$FDO = [3.1374 - (0.1798*MAXW) + (0.2630*DOC)]$$

where FDO = dissolved oxygen concentration available to eggs for hatching stimulus, MAXW = maximum water temperature, and DOC = dissolved oxygen concentration of the pool. The coefficients of this equation indicate that a smaller eddy coefficient should be used (0.3 instead of 0.6 utilized in the simulation model) and the value for increased uptake of dissolved oxygen by bacterial metabolism. These changes, in addition to the replacement of average water temperature with maximum water temperature, produced values in the model that were more compatible with field observations. The proportion of variation explained by these coefficients is 0.4312.

There is reason to believe that change in oxygen levels rather than absolute levels is the stimulating factor in egg hatch (Judson, 1962). The model now uses change in oxygen level to stimulate hatch but utilizes an equation derived from the previously mentioned author's work on static oxygen levels and their effect on transition from the egg stage and survival to instar I. This is, no doubt, resulting in a reduced hatch in the computer simulation but insufficient data concerning the mechanics of this process negates any change in the model at this time.

Water Depth

A correlation of 0.8391 was obtained for the simulated and actual field data which indicated a reasonable model for seasonal inundation of the microbasin area. Correspondence between daily values varied during the study period with simulated depth increasing and decreasing at a faster rate than observed field conditions. This suggested that real pool depth depends, to a large degree, on water table levels during spring flood conditions. This is in agreement with Horsfall's (1963) contention that the level of the water table is an important factor in the flooding of a microbasin area and, in addition, the ability to retain additional input of water as a result of snow melt and/or precipitation. No data was available concerning fluctuation of water table depth at the study site so substantial refinement of this component was not undertaken.

Footnotes

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[2]VARIABLE NAME used throughout the paper are the actual variable names utilized in the computer program.

[3]Since we are using FORTRAN language for the equations contained in this paper, (VARIABLE NAME)** X represents a given quantity raised to the X^{th} power.

Table 1. Age structure of a population of univoltine Aedes mosquitoes[a]

Month	Week	Proportion of Population Completing Indicated Number of Gonotrophic Cycles					Proportion of Population Laying Eggs
		0	1	2	3	4	
June	3	0.7	0.3				0.3
	4	0.4	0.6				0.3
July	1	0.1	0.9				0.3
	2		0.7	0.3			0.4
	3		0.6	0.3	0.1		0.2
	4		0.4	0.2	0.3	0.1	0.6
August	1		0.3	0.3	0.2	0.2	0.2

[a]Modified from Shlenova and Bey-Bienko, 1962.

Table 2. Correlation matrix for max-min air and water temperatures and dissolved oxygen concentration in a woodland pool ecosystem at Yankee Springs recreational area, 1973

	Dissolved Oxygen	Max Water Temp	Min Water Temp	Max Air Temp
Max water temp	-0.5923			
Min water temp	-0.3792	0.7526		
Max air temp	-0.5090	0.8775	0.7107	
Min air temp	-0.4414	0.7260	0.8542	0.8285

Fig. 1. Flowchart of *Aedes* population dynamics as expressed by the computer simulation model. A. Population dynamics of immature stages. B. Location of key pool dimensions and spring eggs and egg hatch response. C. Dynamics of adult population, egg input response, and location of summer eggs. Subroutine DEVLOP moves totals in all vectors (except egg stage) down from position 1. Subroutines HATCH, GRADUAT, and LAYIT transfer cohort sums as shown by arrows.

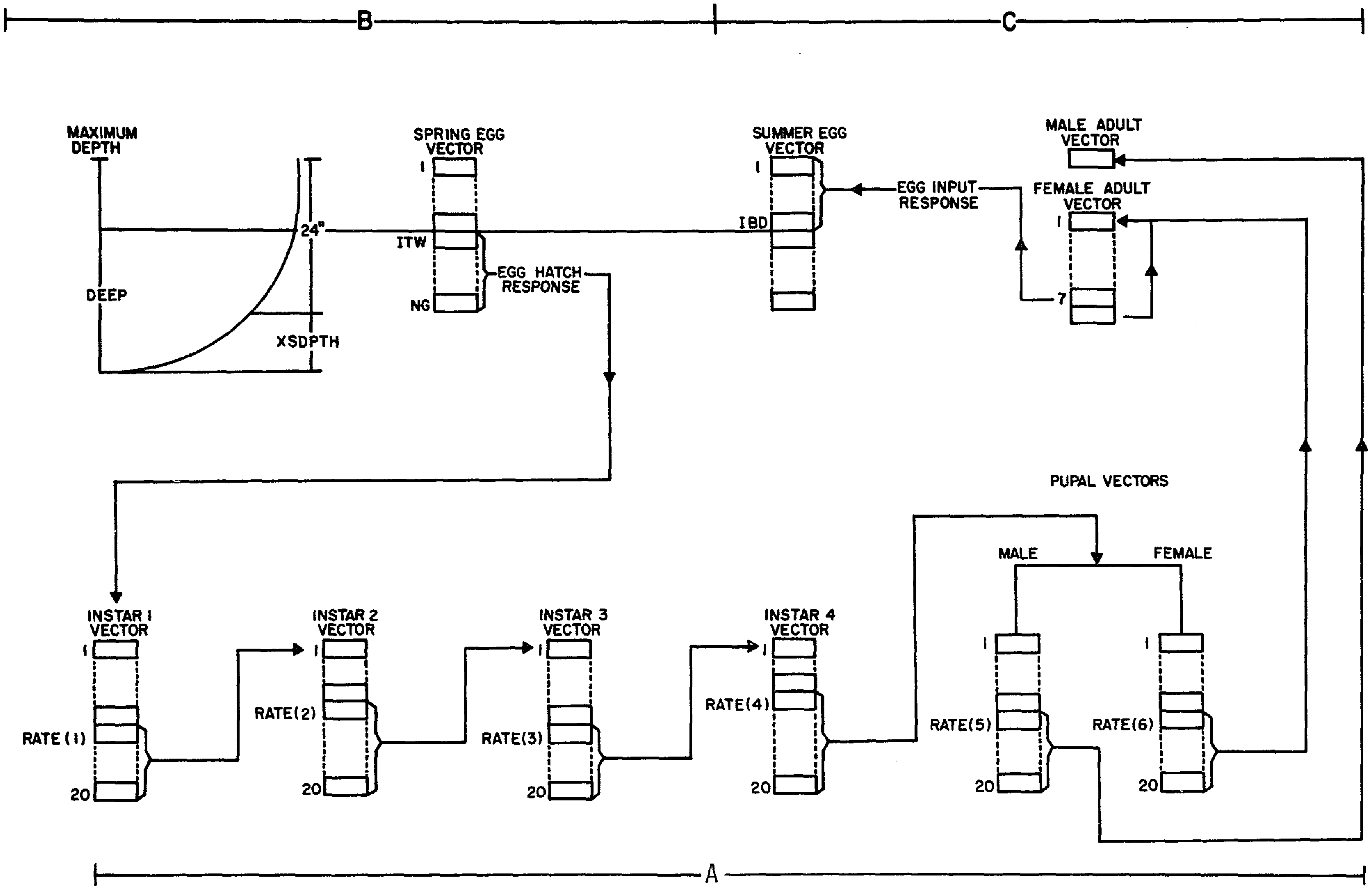
B
C
MAXIMUM DEPTH
24"
DEEP
XSDPTH
SPRING EGG VECTOR
1
ITW
NG
EGG HATCH RESPONSE
SUMMER EGG VECTOR
1
IBD
EGG INPUT RESPONSE
MALE ADULT VECTOR
FEMALE ADULT VECTOR
1
7
PUPAL VECTORS
MALE
FEMALE
INSTAR 1 VECTOR
INSTAR 2 VECTOR
INSTAR 3 VECTOR
INSTAR 4 VECTOR
RATE (1)
RATE(2)
RATE(3)
RATE(4)
RATE(5)
RATE(6)
1
20
A

Figure 1

Fig. 2. Flowchart of the program structure of the *Aedes* computer simulation model.

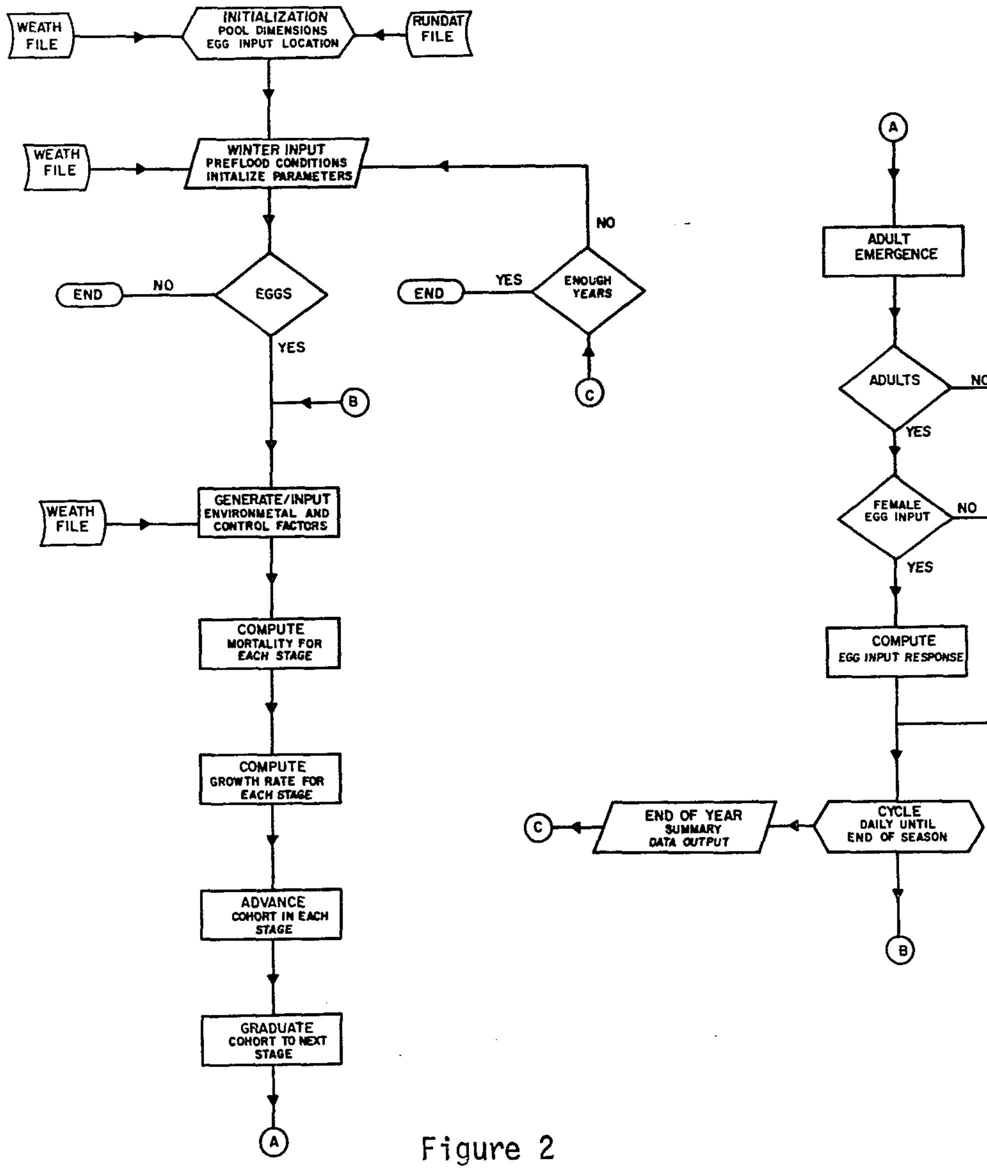
WEATH FILE
INITIALIZATION
POOL DIMENSIONS
EGG INPUT LOCATION
RUNDAT FILE
WEATH FILE
WINTER INPUT
PREFLOOD CONDITIONS
INITALIZE PARAMETERS
NO
END
NO
EGGS
YES
END
YES
ENOUGH YEARS
NO
C
B
WEATH FILE
GENERATE/INPUT
ENVIRONMETAL AND
CONTROL FACTORS
COMPUTE
MORTALITY FOR
EACH STAGE
COMPUTE
GROWTH RATE FOR
EACH STAGE
ADVANCE
COHORT IN EACH
STAGE
GRADUATE
COHORT TO NEXT
STAGE
A
A
ADULT
EMERGENCE
ADULTS
NO
YES
FEMALE
EGG INPUT
NO
YES
COMPUTE
EGG INPUT RESPONSE
C
END OF YEAR
SUMMARY
DATA OUTPUT
CYCLE
DAILY UNTIL
END OF SEASON
B

Figure 2

Fig. 3. Survivorship curves for *A. stimulans-fitchii* adults at Yankee Springs recreational area, 1972-1973 (semi-log, 2 cycles x 10 divisions).

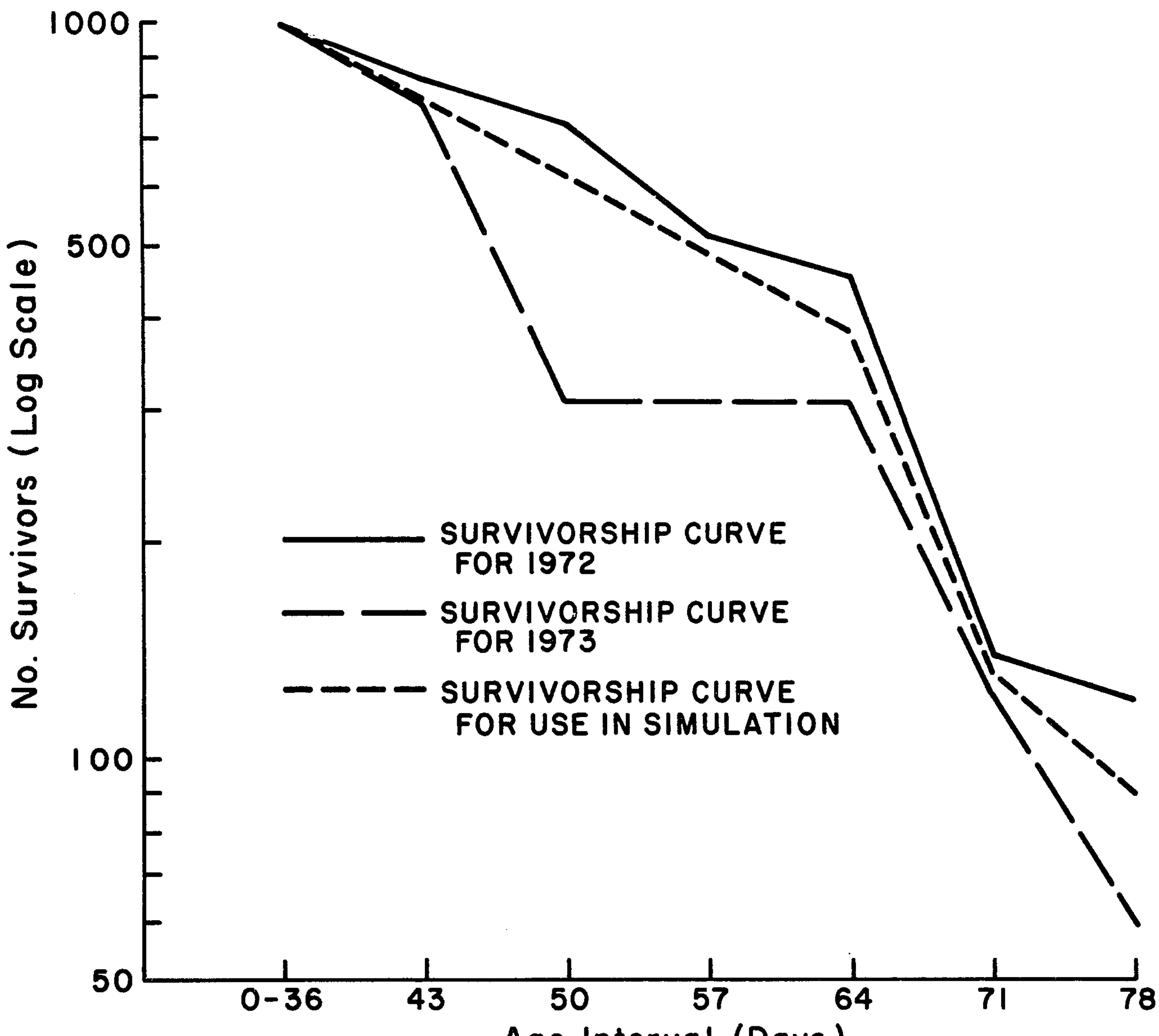
1000
500
100
50
No. Survivors (Log Scale)
SURVIVORSHIP CURVE FOR 1972
SURVIVORSHIP CURVE FOR 1973
SURVIVORSHIP CURVE FOR USE IN SIMULATION
0-36
43
50
57
64
71
78
Age Interval (Days)

Figure 3

SUMMARY AND CONCLUSION

Mosquito biting activity was studied in Michigan parks from 1971 to 1973. The results indicated that woodland Aedes mosquitoes were the pest species in the majority of state parks. Adult collections at North Higgins Lake Park and Yankee Springs recreational area during 1972 and 1973 revealed A. communis-trichuris and A. stimulans-fitchii species complexes, respectively, were the major mosquito pests. Populations of the former species complex were relatively short lived with highest biting activity occurring late May. Populations of A. stimulans-fitchii existed until late August with highest biting activity occurring late June and July. Preliminary observations on effect on human recreation at the two parks showed planned recreational activities were cancelled during periods of high mosquito biting activity.

Studies were also conducted during 1972 and 1973 at Yankee Springs on population dynamics of A. stimulans-fitchii mosquitoes.

The results of field studies indicated extreme daily variability in immature mosquito dynamics as well as weather conditions from March 1 to April 15. Examples included serial egg hatch over a 14 day period resulting in the addition of first instar cohorts and an immature population consisting of all four instar stages during the month of April. Biological and physical parameters were much more stable in late April and early May. The water depth in the pool was steadily receding and all cohorts were in the late instar stages of development and uniform in distribution and composition. The former phenomenon was due to the progressively decreasing pool depth which constricted the larval population into a smaller geographical area. The more uniform instar composition previous to adult emergence was due to the warmer water temperature which accelerated growth rates of all immature cohorts. Seasonal inundation of the microbasin area was consistent for the two years with the highest water levels measured in 1973. This was a factor in determining immature population densities as the higher population totals in 1973 were due to the flooding of additional egg containing soil gradients of the pool. Overall mortality was approximately 0.75 for both years with the highest rates observed in the late instar stages. As the rate of larval development and biomass increase was rapid in a temporary aquatic ecosystem, nutrient restrictions placed on immature mosquito populations would explain the substantial attrition during later developmental stages.

Adult female populations were comparable for the two year period with slightly higher totals in 1973. Peak population levels were maintained for approximately one month after emergence with substantial mortality occurring during July and August. A plot of survivorship curves for 1972 and 1973 showed that the A. stimulans-fitchii female population had minimum mortality for most of the adult life span. High losses occurred primarily among the older females which indicated mortality rates were age dependent. The significance of this data is that the ability of this mosquito to exist at high population levels for so long made it a potential disease vector as well as the insect pest responsible for continual disruption of recreational activities throughout the summer months.

The results of field studies conducted at Yankee Springs recreational area on populations of A. stimulans-fitchii mosquitoes were used in validation of the computer simulation. This was the process of gaining confidence that the model represented its real counterpart in the natural ecosystem. Once the model was refined with data from the study, deviation between the simulated and observed larval responses was small enough to result in adequate correspondence of the model's internal structure to that of the real system. Simulation values for the biological components representing the immature stages showed the daily variability from March 1 to April 15 that was observed in the actual field studies. Examples of the model's responses included: Twofold increase in water depth during 48 hours; serial egg hatch over a 14 day period resulting in the addition of five first instar cohorts; and an immature composition of all four instar stages in early April. However, the modeling approach indicated deficiencies in research and/or lack of information on the actual dynamics of certain biological components of the Aedes ecosystem. This was especially true of egg-laying behavior and larval and egg mortality. The model's approach to these behavioral features was purely speculative and implications for the design of experiments to obtain improved estimates are obvious. The same can be said for simulation values representing physical features of the woodland pool. The low proportion of variation explained by the model for dissolved oxygen concentration indicated the dynamics of this aquatic feature was not well understood and resulted in a reduced egg hatch in the computer simulation. Values for oxygen levels were probably being underestimated but insufficient data precluded an improved parameter estimate. Although there was a high correlation between simulated and actual values for water depth, daily correspondence between these values varied with simulated depth increasing and decreasing at a faster rate. The model did not take into consideration the level of the water table, an important factor in the flooding of a microbasin area. Experiments conducted to understand fluctuation of water table levels during spring flooding would result in substantial refinement of this component. As a result predictions on immature larval populations in a given year could be made with greater precision.

The strong point of this modeling process was that for the first time an attempt had been made to look at the life cycle and physical parameters of woodland Aedes mosquitoes through a systems science approach. Research in the past has taken a haphazard approach with numerous research projects concerned with various aspects of the life cycle but no attempt was made to show how the results related to the entire life cycle. The Aedes model is so constructed that if an assumption concerning a component proved invalid, that portion of the model can be replaced by the correct functions. This modular approach insures that the model will remain a useful working tool. One use of the system model in the future will be in the area of pest management.

Preliminary analysis of the computer simulation has shown that immature mosquito larvae are quite sensitive to alteration of physical parameters of the aquatic ecosystem. What makes sensitivity analysis so interesting is that it considers the Aedes system as a whole and very often a change in one system parameter produced an unexpected change in another. As a result, sensitivity analysis can provide a framework for pest management decisions. Another future consideration is the use of the simulation in the study of viral multiplication in the mosquito. Little information is available concerning the mechanism of viral buildup in the invertebrate vector. A model could be constructed utilizing current research data and coupled to the woodland Aedes model to simulate viral activity in the mosquito. As results of subsequent research become available, more valid functions can be substituted.

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